NEST PREDATION OF GROUND-NESTING BIRDS IN MEDITERRANEAN FARMLAND: AFFORESTATION EFFECTS AND MAIN PREDATORS

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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

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Summary

Habitat fragmentation is one of the main threats to global biodiversity. It can be defined as a combination of habitat loss and isolation to a degree in which the habitat is broken down, affecting distribution, reproduction and survival rates of species differently and potentially leading to local extinction. Edges effects, which increase with fragmentation, may play a critical role in determining the impacts of afforestation, leading to changes in species richness, abundance and composition in terms of both predator and prey. In the Mediterranean farmland, several grassland birds respond negatively while other farmland species respond positively to edges resulting from recent afforestation processes due to a period of drastic socioeconomic changes. Simultaneously, a process of increasing agricultural intensification occurred and shaped farmland birds' response. Nest predation, one of the most selective pressures in nature, is reported as severely influenced by these changes to local and landscape context.

We experimentally evaluated some of the main defining variables that influence nest predation in the Mediterranean farmlands of Castro Verde and tried to identify patterns in nest predation through the identification of predator species. To do this, we used artificial nests placed at 100 m intervals across 51 experimental parcels of Mediterranean farmland consisting of a transect through woodland (Pine, Eucalyptus and Oak stands), edge and open grassland. Camera traps were used during seven days to identify nest predators. To test the effect of manipulation on artificial nests with camera, two additional different nests were used, controlling for both camera use and vegetation manipulation.

A total of 48.6% of nests were predated, with higher predation happening in pine stands (52.6%) which resulted from recent afforestation processes and are known to cause higher impacts on biodiversity due to its contrast with natural Mediterranean woodland. Predation was also more frequent near the edge, overall (52.8%). However, landscape type appeared to be more influential than edge effects *per se*. Manipulated nests were more frequently predated than non-manipulated ones, especially in camera control treatment (55.9%). The most influential variables for predicting predation rates were nest site manipulation, vegetation height and occurrence of Carrion crow. Predation probability highly decreased with increasing vegetation height, while manipulating nest-sites severely increased predation probability, overall reflecting the importance of nest conspicuousness. Landscape variables did not show a significant

influence on predicting predation patterns. Seventeen species were identified with cameras, although nests associated with camera use resulted in different predation rates than those without it. Approximately 50% of identified predators were corvids, a generalist group of predators known for their ubiquity and increasing tendencies in novel plantations due to their exploratory behaviour.

We found that nest predation rates in Mediterranean farmlands of Castro Verde were shaped, to an extent by a limited set of local variables and the abundant presence of corvids. To improve on our knowledge and predictability of these patterns, more extensive characterization of predator identity in each landscape is an expensive but determining factor, when considering future success of targeted management and conservation efforts.

Keywords: habitat fragmentation; edge effects; agricultural intensification; nest predation; artificial nests; camera traps; corvids; Mediterranean farmland; Castro Verde.

Sumário

A fragmentação de habitat é uma das principais ameaças à biodiversidade global. Pode ser definida como uma combinação de perda de habitat e isolamento até um grau em que o habitat fica dividido, afetando as taxas de distribuição, reprodução e sobrevivência da espécie de maneiras distintas e levando a uma potencial extinção local. Efeitos de orla, que aumentam com a fragmentação, podem desempenhar um papel crítico na determinação dos impactos da florestação, levando a mudanças na riqueza de espécies, abundância e composição em termos de predador e presa. Nas terras agrícolas da região Mediterrânea, várias aves associadas a meios agrícolas (*e.g.,* pastagens) reagem negativamente, enquanto outras espécies de campos agrícolas reagiram positivamente às orlas resultantes de processos de florestação recentes devido a um período de mudanças socioeconómicas abruptas. Ao mesmo tempo, um processo de crescente intensificação agrícola ocorreu, contribuindo para definir a reação das aves afetadas. A predação de ninhos, uma das pressões mais seletivas na natureza, foi severamente influenciada por estas alterações ao contexto local e de paisagem.

Avaliámos experimentalmente algumas das principais variáveis que influenciam a predação na região Mediterrânea de Castro Verde a nível local e da paisagem, procurando ao mesmo tempo identificar padrões na predação através da identificação de espécies de predadores. Para tal, utilizaram-se ninhos artificiais colocados a intervalos de 100 m ao longo de 51 parcelas experimentais de terras agrícolas no Sul de Portugal, consistindo num transecto feito ao longo de floresta (pinhais, eucaliptais e sobreirais/azinhais), orla e pastagem. Para tal utilizámos armadilhagem fotográfica durante um período de sete dias para identificação de predadores. Para testar os efeitos de manipulação nos ninhos com câmara, dois outros ninhos foram usados, controlando tanto para uso da câmara como para a manipulação da vegetação.

Um total de 48,6% dos ninhos foram predados, ocorrendo um nível mais alto de predação em povoamentos de pinheiro (52,6%) que resultam de processos de florestação recentes e são conhecidos por causar maiores impactos sobre a biodiversidade, devido ao seu contraste com a floresta autóctone. A predação também foi em média mais frequente perto da zona de orla (52,8%). No entanto, o tipo de floresta adjacente pareceu ser mais influente do que os efeitos de orla em si. Ninhos manipulados foram mais frequentemente predados do que os não-manipulados, especialmente no tratamento de controlo da câmara (55,9%). As variáveis mais

influentes para prever as taxas de predação foram altura da vegetação em redor do ninho, a manipulação do local do ninho e a ocorrência de Gralha-preta. A probabilidade de predação decresceu marcadamente com o aumento da altura da vegetação, enquanto que a manipulação dos locais em redor do ninho levou a um grande aumento na probabilidade de predação, revelando assim a importância da conspicuidade para os ninhos. Variáveis da paisagem não mostraram uma influência significativa na previsão de padrões de predação. Dezassete espécies foram identificadas com câmaras. Todavia, ninhos em que houve utilização da câmara pareceram demonstrar diferentes taxas de predação relativamente a ninhos sem esta. Aproximadamente 50% dos predadores identificados foram corvídeos, um grupo de predadores generalistas, conhecidos pela sua omnipresença e rápida adaptação às plantações florestais, devido ao seu comportamento exploratório.

Descobrimos que as taxas de predação na zona de Castro Verde foram moldadas, em certa medida, por um conjunto limitado de variáveis locais e pela abundante presença de corvídeos. Para melhorar o conhecimento e previsibilidade destes padrões, uma caracterização mais extensa da identidade da predação em cada paisagem é um fator que apresenta elevados custos, mas determinante, quando se considera o futuro sucesso dos esforços de gestão e conservação deste tipo de meios.

Keywords: fragmentação de habitat; efeitos de orla; intensificação agrícola; predação de ninhos; ninhos artificiais; armadilhas fotográficas; corvídeos; agricultura no Sul da Europa; Castro Verde.

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Abbreviations

ACP: Annual Crops and Pastures;

AWMSI: Area-weighted Mean Shape Index;

CAP: Common Agricultural Policy;

CI: Confidence Interval;

COS2007: Carta de Uso e Ocupação do Solo de Portugal Continental para 2007;

EEC: European Union Eco-regulation;

GIS: Geographic Information System;

GLMM: Generalized Linear Mixed Model;

m.a.s.l: meters above sea level;

OW: Open Woodland;

PC: Permanent Crops (not to be confused with PC1-6 which refers to Principal Components);

PCA: Principal Component Analysis

SPA: Special Protection Area;

s.d.: Standard deviation;

SE: Standard Error;

“It's the questions we can't answer that teach us the most. They teach us how to think. If you give a man an answer, all he gains is a little fact. But give him a question and he'll look for his own answers”

Patrick Rothfuss

1. Introduction

In this section I will provide an overview on the concepts necessary to understand the framework upon which this thesis is inserted. We will briefly touch on the subject of Habitat fragmentation and the different aspects that are directly connected and influence or are influenced by this concept, namely, Edge effects, Afforestation and Agricultural Intensification. Finally, we will focus on Nest predation, which is influenced by the resulting impacts of the aforementioned concepts and is the main target of this study.

1.1. Habitat Fragmentation and Loss

Concept

Habitat fragmentation is often considered as one of the most important factors contributing to species decline or loss worldwide (Noss & Cooperrider 1994; Brook *et al.* 2003; Lindenmayer & Fischer 2006) and, therefore, one of the main threats to global biodiversity (Fischer & Lindenmayer 2007) negatively affecting most taxonomic groups such as mammals and birds (Andrén *et al.* 1997; Patterson *et al.* 2016), reptiles (Gibbon *et al.* 2000), amphibians (Stuart 2004) and even plants (Aguilar *et al.* 2006).

The concept of Habitat Fragmentation can be defined as a combination of 'habitat loss' and 'habitat isolation' or sub-division (Forman 1995) and one should look at it from two distinctive but connected perspectives. Both as a process: that which causes fragmentation or, as Franklin *et al.* (2002) put it, as a "set of mechanisms leading to the discontinuity in the spatial distribution of resources and conditions present in an area at a given scale that effects occupancy, reproduction and survival in a particular species"; and as an outcome: the state of being fragmented (Wiens 1994; Franklin *et al*. 2002).

Authors initially explored and interpreted habitat fragmentation as an island type phenomenon viewing patterns like species richness and abundance in an 'island biogeography' or 'percolation theory context' (Forman *et al.* 1976; Opdam & Wiens 2002) but this is not completely correct since, unlike real islands, habitat fragments are seldom surrounded by such ecologically homogeneous environments. In the context of habitat fragmentation, the influences of surrounding landscape are as important, if not more, than those of the fragment itself (Wiens 1994).

Also frequent is the use of fragmentation and heterogeneity as the same concept. In fact, the outcome of fragmentation is binary (in the sense that the resulting landscape is composed of fragments and something else such as, for instance, fragments of a

forest and a non-forest matrix between them. As for heterogeneity, it implies a multi-state outcome from some sort of disturbance (usually a natural one). For example, a fire could transform a previously contiguous forest into a mosaic of different vegetation stages which in turn could each be perceived as a distinct habitat by a certain species resulting in habitat heterogeneity with consequences in habitat quality (Franklin *et al.* 2002), although they would not necessarily be bad. Heterogeneous modified landscapes support more species than otherwise similar but less heterogeneous landscapes due to their residual complexity (Tscharntke *et al.* 2005). For instance, landscape heterogeneity is recognized as beneficial for native species of European farming landscapes (Benton *et al.* 2003). Essentially, habitat fragmentation is about heterogeneity in its simplest, binary form of habitat and non-habitat, both influencing one another. Throughout this thesis I shall, for simplicity purposes refer to the term '*Habitat fragmentation'* as one that encompasses both terms.

It's important to understand however, that habitat fragmentation is often only considered significant when habitat loss reaches a point where the continuity between an habitat is broken down (Opdam & Wiens 2002). Franklin *et al.* (2002) argued that not only does the habitat need to be separated by non-habitat but occupancy, reproduction or survival of a species should be affected, either positively or negatively. As landscapes become progressively fragmented, an increasingly greater number of fragments of varying shapes and sizes are created. But fragmentation is not just a principle of patch-level phenomenon, although this is normally the scale at which many of its biological impacts are perceived since the general interest of its study are the anthropogenic impacts that often provoke land use and landscape changes by creating patchworks where continuous native habitats could previously be found. This in turn leads the formation of landscape mosaics, composed by open fields, secondary vegetation and patches of the remnant habitat (see Wilcox & Murphy 1985; Franklin & Forman 1987).

Different scales

Consequently of its anthropogenic impacts in several areas, usually due to agriculture and forestry developments, countermeasures are usually applied at a scale that is relevant to humans. However, the appropriate ecological scale should vary with both organisms and questions implied, since both will affect the way we think and act about fragmentation in several ways (Levin 1992). Franklin *et al.* (2002) suggested a hierarchical scale similar to that established by previous researchers when trying to understand distributional patterns and habitat selection. Habitat fragmentation could

thus be considered at a range-wide scale when occurring throughout a species geographic distribution, at a population scale where it occurs within populations connected by varying degrees of animal movement, and lastly, at a home-range scale for fragmentation occurring within home ranges of individuals. This of course could be finer subdivided but scale-dependency would still be a constant indicator of the change of processes predominating at each scale for a given species. For instance, an occurrence of fragmentation could affect the foraging site of an individual (within its home-range) but not necessarily disrupt the ability of the offspring of the same individual to disperse across a wider area. An ideal gradient of scale would be a continuous one. And while this has been previously proposed, in the form of a spectrum with one end defined by geographical fragmentation and the opposite one by structural fragmentation (Lord & Norton 1990), it unfortunately lacks the biological connection aspect that the other species-centered model includes.

Spatial and temporal scales must also be considered. The first one refers to the distance between habitat patches relative to the dispersal distance of the organism in question and can be characterized by “grain” and “extent” while the later refers to habitat lifespan relative to the generation time of said organism or species (Fahrig 1992).

Landscapes and their contained populations are not stable through time, changing over small and large-scale disturbances such as lighting fires and insect outbreaks but also anthropogenic causes like forest cutting and abandonment of agricultural fields. Vegetational regeneration also causes changes in fragments over time. Therefore, it is only natural that considering a study taking place over one year may yield far different results in their population effects than one considering a decade or a century of the fragmentation process (Wiens 1994), which is especially important when we are dealing with conservation of highly fragmented landscapes (Hilty *et al.* 2006). This is in line with the findings of Fahrig (1991, 1992) implicating the larger importance of temporal over spatial scale. Note however that habitat fragmentation can be static, for instance when resulting from topographic differences (Franklin *et al.* 2002).

Causes and Consequences

While we have briefly touched upon the consequences of Habitat fragmentation by trying to define its concept, it is important that we understand, at least in a general manner, what are the causes and consequences of Habitat fragmentation.

As previously stated, we can have both natural and human-induced fragmentation. The first one generally acts over larger areas and a larger period of time although it can

extend from something close to an instant to phenomena occurring over centuries (*e.g.,* volcanoes, avalanches, glaciations), while also occurring in different frequencies. This results in an altered landscape mosaic (Hilty *et al.* 2006). The second is quite contrasting since it is often rapid and recent (*e.g.,* afforestation of an open-habitat, building roads and houses). Thus, it is quite possible that, for the same environment, we get severely different impacts of these two types of fragmentation (Reino *et al.* 2009).

Habitat isolation is also an important issue that is often related with habitat fragmentation since from the breaking of larger patches into smaller ones we often get isolated patches remaining. This should be regarded as the contrary of habitat connectivity which can broadly refer to the connection of different habitat patches for a given individual species (Fischer & Lindenmayer 2007). Like habitat fragmentation, this occurrence is also believed to contribute to a general decreasing of diversity within the original landscape (Wilcox & Murphy 1985; Murcia 1995; Reino *et al.* 2009). However, there is some evidence that several species are adapted to heterogeneous and fragmented landscapes but surely many more that suffer adverse consequences, especially from human-induced changes that provoke habitat fragmentation (Wiens 1989). Briefly, fragmentation reduces the size of local habitat patches and connectivity among them, thus increasing edge and isolation effects. These in turn make species more susceptible to extinction, although to varying degree that is also dependent on environmental variability, demographic stochasticity and genetic influences (Fischer & Lindenmayer 2007; Reino *et al.* 2013). Another consequence is the possibility of species absence from landscapes where there is still otherwise suitable and favorable habitat that has become too small or isolated (Reino *et al.* 2013). The degree to which either fragmentation or isolation are responsible for these effects and consequent species distributions at larger scales is still debated to this day, despite suggestions from the last cited authors that fragmentation processes at the landscape level may in fact affect large-scale species distributions.

Species-oriented approaches and Pattern-oriented approaches

When trying to understand the effects of habitat fragmentation or other types of landscape modification, two extremes can be identified along a continuum of approaches. The first is a species oriented one, which is normally centered on an individual species believed to respond in an individualistic manner to their environment (Austin & Smith 1989; Fischer & Lindenmayer 2007), its main limitation being the impossibility of conceivably studying every single species in any given landscape. The

latter approach is a pattern-oriented one. These tend to focus on the human-perceived landscape patterns and their correlation with measures of species occurrence in order to infer potential ecological causalities. For instance, a large amount of variability in ecological patterns around edges of fragmented habitat can be explained by distinguishing between four main mechanisms, namely: ecological flows, access to spatially separated resources, resource mapping and species interactions (Ries *et al.* 2004). In this case, the main limitation is that aggregating several species and ecological factors may lead to a significant under-appreciation of the real complexity at hand and result in neglecting a group of species or ecological processes that might be of key significance (Fischer & Lindenmayer 2007).

Species response to habitat loss and fragmentation

Wiens (1989) suggested that the difference in species' responses to habitat fragmentation is dependent on the characteristically individual spatial requirements for edge versus interior locations in habitat patches. Although there is, in general, strong evidence that larger patches are often associated with more species (Lindenmayer & Fischer 2006) and a higher population density (Ewers & Didham 2007), which equates to lower density and species diversity in small disjoint cores in comparison with a single contiguous core of the same total area. Nonetheless, a species may be absent from a fragment or patch of a certain size for a variety of reasons not necessarily related with its area (*e.g.,* failure to colonize or inadequate resources). An example from Santos *et al.* (2002) conducted in the Mediterranean Iberian forests, showed that the capabilities of small woodland patches maintaining populations of forest birds was distinctively lower than patches of equivalent size in more mesic European localities. Which is in line with the general rule stating that individuals will not occupy sites that fall below a certain threshold that defines an adequate area or territorial space (Wiens 1989) and this threshold will vary considerably depending on species, as well as other variables such as affinity for edges versus habitat interiors (Wiens 1989; Reino *et al.* 2013). In fact, the very essence of habitat fragmentation is that not only habitat patches are reduced in size but their proportion of contact with other habitat types (defined as edges, see below) increases. Thus, changes in patch size and shape will sometimes lead to the loss of interior species, contrasting with an increase in species better adapted to edges and also those associated with adjacent habitat types (Tews *et al.* 2004; Reino *et al.* 2009, 2013). This might in some cases contradict the aforementioned general trend, in which less fragmentation means more diversity.

Habitat fragmentation is also a cause for habitat loss, a serious threat to species around the world (Kerr & Deguise 2004; Dobson *et al.* 2006; Hovick & Miller 2013). This is a phenomenon that generally coincides with other threats like habitat degradation, sub-division and other processes (*see* Liu *et al.* 2007). Degraded habitats constitute an 'ecological trap' to which individuals of a given species are attracted but in which they are not able to reproduce (Battin 2004) due to a gradual deterioration of habitat quality (Hazell *et al.* 2004).

We previously defined habitat fragmentation as a combination of habitat loss and isolation. This habitat sub-division can negatively affect day-to-day movements of a given species (for instance, movements between nesting and foraging resources) and even the dispersal of juveniles (Beier 1995; Luck & Daily 2003). In addition, isolation may negatively affect large-scale movements of species such as seasonal migration or range shifts in response to another imminent factor that is climate change (Soulé *et al.* 2004).

Potential consequences on populations and communities

Most studies of the effects of habitat fragmentation on animal communities have been conducted using bird species in temperate forests (Santos *et al.* 2002; Opdam & Wascher 2004; Carrascal *et al.* 2014).

Research conducted in Europe would normally focus on factors operating only at a local shape and habitat structure, such as connectivity (Opdam 1991; Bender *et al.* 1998). Only more recently, authors started considering larger scales when analyzing habitat fragmentation (Santos *et al.* 2002; Reino *et al.* 2013) since several studies suggested, for example, that negative effects of fragmentation seem to be stronger in Mediterranean Europe than Central Europe (Harrison & Bruna 1999; Opdam & Wascher 2004), which is probably related to most areas in Mediterranean Europe being arranged in 'islands' often isolated from the mesic conditions suitable for forest habitats that are generally widespread over most of central Europe (Aronson & Blondel 1999). Furthermore, consequences of large open patch preferences might go as far as to influence the general distribution of species in such places, especially outside species core distribution (Reino *et al.* 2009, 2013).

Local extinction is another major consequence of habitat fragmentation. This is due to an increase in the influence of stochastic events on the availability of resources and other population life traits within a given patch, which enhances the likelihood that a given species may disappear from a fragment (Wiens 1989). Fahrig (2003) hypothesized a direct relationship between habitat loss and fragmentation with the

predicted occurrence of the extinction threshold. Despite the ambiguity noted by the author in the interpretation of this threshold, it emphasizes the relationship between the effects of habitat fragmentation and habitat loss. Thus, we can infer that the species loss that frequently accompanies fragmentation is usually non-random. For instance, larger species of birds such as those of high trophic position are usually more prone to extinction (Purvis *et al.* 2000; Carrascal *et al.* 2014), which may be explained by their low frequency of occurrence among patches and low abundance (Wiens 1989). It is also possible for cascading effects to occur on native species, especially when concerning 'keystone species' such as those of high trophic position since they exert a disproportionate effect on ecosystem function relative to their abundance (Paine 1969; Soulé *et al.* 2005), resulting from simultaneous reduction of the total amount of native vegetation and landscape connectivity (Fischer & Lindenmayer 2007). Extinction cascades happen when the extinction of one species triggers the loss of another, leading to a cascading effect of potentially several species extinctions (*e.g.,* Terborgh *et al.* 2016).

1.2. Edge effects

An overview

Fischer & Lindenmayer (2007) defined edge effects as "the changes in the biological and physical conditions at an ecosystem boundary or within adjacent ecosystems". Changes in physical variables such as moisture, temperature, wind speed and soil nutrients constitute abiotic effects, while biotic effects are changes in biological variables such as species composition of plants and animals, patterns of predation, parasitism and composition.

Large amounts of variety in the ecological patterns around edges are thought to be explained by a few distinguishing fundamental underlying mechanisms: habitat structure, food availability and species interactions near edges (Ries *et al.* 2004).

Habitat edges can influence an array of population and community processes. From dispersal rates to species interactions (Fletcher 2005), edge effects were also reported on playing a critical role in determining impacts of afforestation and changes of species richness and composition (Ries *et al.* 2004; Ewers & Didham 2007) often leading to increased nest predation rates (reviewed in Batary & Baldi 2004), although not always (see Huhta *et al.* 2015).

Indeed, there are several factors that enhance or simply change the magnitude of

edge effects and ecological processes near habitat edges often differ from the processes away from edges (Donovan *et al.* 1997). These authors found that the effect of edges is not the same in all landscape conditions, with effects for instance in nest predation patterns being dependent, at least in part, on landscape context. Edge effects influenced nest predation patterns only for highly and moderately fragmented landscapes, which was not particularly dependent on predator composition, whereas a study in forest landscapes with temporarily open clear-cuts did not reveal edge effects on predation rates (Huhta *et al.* 2015).

Consequences on general Species distribution

Species distribution can be severely influenced by the nature of the matrix habitat, which plays a major role in determining the strength of edge effects (Ewers & Didham 2007; Huhta *et al.* 2015). Furthermore, a high structural contrast at the edge (soft edge vs. hard edge) amplifies known effects (Ries *et al.* 2004) to a degree which may be intensified according to landscape fragmentation and the shape of fragments, due to cumulative effect of multiple edges (Fletcher 2005).

There seems to exist a strong positive relationship between fragment area and shape complexity of forest fragments, and these in turn seem to have consequences on edge-penetration distance thus affecting the amount and distribution of core habitat available for species threatened by edges (Ewers & Didham 2007).

Such effects lead to strong impacts in both magnitude and extent on edge effects, influencing bird distribution in highly fragmented landscapes. Shape complexity effects in an increasing fragmented area can have such a dramatic impact that it overrides the area effect to the extent that the usual negative relationship between density and area is reversed, leading to a potential reduction in population size of core-dwelling species by 10 to 100%, depending on their sensitiveness, while edge-dwelling species benefit from this shape complexity (Ewers & Didham 2007). High wind speeds and temperatures or exotic and invasive taxa may also influence and modify the impacts on species at a landscape level (Harper *et al.* 2005). With this, it is natural that many species are absent or scarce near edges and also expected to decline with increasing edge density and smaller, more convoluted patches (Ewers & Didham 2007; Reino *et al.* 2009). Simultaneously, a number of edge-dwelling species use these edges to their advantages, therefore tending to be more prevalent in more fragmented landscapes, (Bender *et al.* 1998; Reino *et al.* 2010a).

Edge effects in the Mediterranean farmland

Due to the aforementioned conditions, as well as synergistic effects between edge and the habitat areas themselves, it becomes possible for habitat edges to be richer in species than either of the adjacent habitats (Ewers *et al.* 2007). But the opposite is also a viable situation where species richness increases with distance to edges (Ewers & Didham 2006), depending on which conditions in terms of ecological patterns are met (for instance, assemblage composition and their individual responses to edges). A situation reflecting both ends of the spectrum was found in the region of Castro Verde, where typical farmland birds, such as Galerida larks (*Galerida theklae*, *G. cristata*) and Corn buntings (*Emberiza calandra*), tended to reach high densities closer to edges and thus apparently benefited from increasing landscape fragmentation, whereas edge avoiders such as Calandra larks (*Melanocorypha calandra*) were only abundant over large open farmlands (Reino *et al.* 2009). In this particular study, only the steppe birds (open grassland specialists) showed marked negative responses to wooded edges. This further supports the claims of some authors, whom have also found a lack of edge effects *per se* within grassland habitats, which they considered reflected the range of foraging behaviour of edge predators and the presence of resident grassland predators, creating an effect of pooling species with contrasting edge responses (Batary & Baldi 2004; Reino *et al.* 2009, 2010a; b). For instance, Reino *et al.* (2010b) found predation rates to peak in landscapes with intermediate edge densities, influenced by a stronger relationship with landscape context (type of plantations and overall forest plantation cover) than with edges themselves, which is further supported by claims that it is the alteration of the matrix surrounding the forest rather than just the presence of land without forest, which influences factors such as nest predation rates (Stirnemann *et al.* 2015). The value of investigating edge effects is thus further extended when trying to understand the impacts of afforestation on biodiversity (Reino *et al.* 2009).

Finally, the effect of increases in edge density together with higher number of patches observed in landscape-scale studies can be potentially determinant in shaping large scale species distribution over the Iberian Peninsula (Reino *et al.* 2013).

1.3. Landscape modification

Land-use changes and Biodiversity

In the recent past, agricultural landscapes throughout all Europe have suffered dramatic transformations due to a period of increasingly rapid and intense economic and social changes (Vos & Meekes 1999; Jongman 2002). Human activity can profoundly influence and modify land cover and vegetation structure at both levels, consequently affecting composition and abundance of local communities (Sánchez-Oliver *et al.* 2013). Across most of Europe we see a general trend for agricultural intensification and the loss of semi-natural habitats in the most productive regions while on marginal farming areas, land abandonment and afforestation spreads (Donald *et al.* 2006; Aschwanden *et al.* 2007; Pita *et al.* 2009; Kentie *et al.* 2015). Along with habitat fragmentation, these landscape transformations have resulted in major population declines of farmland species across a wide variety of taxonomic groups and geographic areas (Patterson *et al.* 2016). For example, landscape modifications are known to directly influence bird species by causing shorter breeding seasons, laying of fewer eggs and nestlings and might even alter their mating system and movement patterns (Fischer & Lindenmayer 2007). Increased predation and parasitism have both also been frequently reported in modified landscapes, especially in the case of birds (Fischer & Lindenmayer 2007; Beja *et al.* 2014).

Livestock grazing can be a considering factor as well, since it simplifies vegetation structure and exacerbates the replacement of native species by introduced species, while also reducing regeneration rates of native woody vegetation (Hobbs 2001).There are many other land management practices such as logging or firewood collection which can be linked to the deterioration of vegetation structure and the physical environment encompassed by it (Chettri *et al.* 2002; Fischer & Lindenmayer 2007).

Indeed, there is a widespread agreement among several stakeholders that halting biodiversity loss will only be possible through the implementation of land-use strategies that integrate the needs of both human activities and biodiversity conservation (Caro *et al.* 2015). This prompted several initiatives, such as the Common Agricultural Policy (CAP) and, to a more general extent, the LIFE Nature programme, which aimed to make agricultural practices more favourable to conservation in a farmed-landscape context (Aschwanden *et al.* 2007; Sánchez-Oliver *et al.* 2013, 2014; Santana *et al.* 2014). It is important to understand how each of these types of landscape modification affects biodiversity in order to try and find a possible balance among them.

Agricultural Intensification

Haberl *et al.* (2005) hypothesize on agricultural intensification reflecting the strong negative correlation that formed between the human appropriation of net primary production and bird species diversity. Intensification can be achieved through several different processes: increased levels of mechanization and chemical use; changes in the areas of different crop types; the replacement of extensive pastureland by improved pastures; changes in the times of sowing and harvesting; spreading of monocultures; increasing cattle stocking densities; changes in soil moisture and the loss of semi-natural habitats such as temporary ponds or shrubland (Donald *et al.* 2006). Meanwhile, irrigated fields are ever expanding only to be used as fodder crops (Newton 2004; Pita *et al.* 2009). These changes have shown negative impacts on amphibians (Beja & Alcazar 2003), small mammals (Pita *et al.* 2009) and particularly birds (Donald *et al.* 2006). For instance, the range of a characteristic steppe bird, Great bustard (*Otis tarda*), has greatly diminished with the proliferation of intensive agricultural practices and also excessive hunting, since they are known to thrive within diverse habitat mosaics with limited anthropogenic disturbance (Gooch *et al.* 2015). It is important to note, however, that agricultural intensification is not universally deleterious since a small number of species, such as corvids, might benefit from it (Barnett *et al.* 2004).

Agricultural intensification may also have increased the accessibility of grasslands for predators and reduced nest crypsis due to homogeneous swards that are also amplified by early mowing (Evans 2004; Kentie *et al.* 2015).

Afforestation / land abandonment

Since secondary succession usually takes a long time by itself, it is common practice to plant forests on grassland, cropland or shrubland in order to not only speed the process up, but also increase profits from either abandoned lands or otherwise poorly productive soils (Carrascal *et al.* 2014). This process is sometimes used with conservation objectives in mind, such as restoring forest ecosystems in marginal or abandoned farmland (Loyn *et al.* 2007; Reino *et al.* 2009). Indeed, in the European Union, the Common Agrarian Policy (CAP) has favored the transformation of farmland intro tree plantations since 1992 via a scheme of aid for forestry measures in arable landscapes (EEC Council Regulation No. 2080/92), resulting on the afforestation of > 8 million ha by 2013 (“European Commission” 2013), a value that is likely to increase due to several subsidies to vineyard extirpations and afforestations (Sánchez-Oliver *et al.*

2013). Afforestation can be a prominent conservation issue, especially in recent times where Climate change has prompted a great incentive on its large-scale use to reduce atmospheric concentrations of carbon dioxide (Potter *et al.* 2007). It may have severe impacts on biodiversity, for instance, where forests replace open habitats of conservation implication (Díaz *et al.* 1998; Reino *et al.* 2010a) and by increasing nest predation risk in tree plantations with lower tree development (Reino *et al.* 2010a; Sánchez-Oliver *et al.* 2013). Although effects might sometimes be positive, specifically when forest species are the target of conservation efforts (Loyn *et al.* 2007), new plantations are often used by generalist predators and widely distributed species such as corvids and medium-sized carnivores in contrast to the original inhabitant species of these grassland and shrubland habitats (Díaz *et al.* 1998; Pita *et al.* 2009; Reino *et al.* 2009). Recent empirical evidence suggests that these effects may extend beyond forest boundaries since at least some grassland birds strongly avoid forest edges and occur at much reduced densities in fragmented landscapes (Reino *et al.* 2009; Morgado *et al.* 2010). Furthermore, amplitude of such effect varies with different species (Ewers & Didham 2006; Reino *et al.* 2009, 2010b).

The impacts of afforestation arise from the consequential habitat fragmentation, as continuous patches of open-habitat are broken into smaller, isolated patches surrounded by a matrix of forested habitats with the increasing proliferation of edges (Ries *et al.* 2004; Huhta *et al.* 2015). Afforestation impacts are also dependent on assemblage composition and on the conservation value of sets of species and their response to edge effects (Reino *et al.* 2009). Birds represent the most intensively studied group when it comes to these impacts on farmland since they are good indicators of the success of colonization of forest plantation as they are highly mobile and therefore are able to easily reach these novel ecosystems (Carrascal *et al.* 2014; Sánchez-Oliver *et al.* 2014).

Land-use changes in the Mediterranean region

Since the early 1990s, agriculture has become progressively more intensive and this has also contributed severely to the decline of populations of Mediterranean farmland birds and other wildlife across Europe (Donald *et al.* 2006; Pita *et al.* 2009). Land use intensification in Mediterranean farmland has been associated with increases in both the abundance of generalist predators (Beja *et al.* 2009, 2014; Pita *et al.* 2009) and stocking densities (Reino *et al.* 2010b; Beja *et al.* 2014).

Commonly found in the Mediterranean farmland are cereal steppes which result mostly from the cultivation of dry cereal crops and extensive pastures, making them

economically marginal farming systems threatened not only by agricultural intensification in the more productive soils, but also agricultural abandonment and afforestation in poorer soils (Moreira *et al.* 2007).

In the Mediterranean region, afforestations of marginal agricultural land has increased over time, following a long-term trend of rural abandonment of poorly productive soils (Van Doorn & Bakker 2007). Pine (*Pinus* spp.) or eucalyptus (*Eucalyptus* sp.) plantations are now a common practice and they have a strong impact on biodiversity since habitat requirements of bird species characteristic of this dominantly agricultural environment generally contrast with the structural characteristics provided by these plantations, which are known to possess a poor shrub layer and lack of suitable microhabitats in the understory, as opposed to the characteristic broadleaf sclerophyllous foliage or well-developed understory found in autochthonous forests (Tellería & Santos 1999; Carrascal *et al.* 2014).

There are three major types of effects determining bird species identity in the Mediterranean cropland afforestation, namely: regional distribution patterns, habitat preferences of species and autoecological traits related to life history (Carrascal *et al.* 2014). The pseudo-steppes of the Iberian Peninsula cover over 4.5 million ha and are one of the farmland habitat types holding a larger number of bird species with unfavourable conservation status (Bota 2005; Moreira *et al.* 2007). Reino *et al.* (2009) found strong evidence of composition of forest plantations affecting edge responses of bird functional groups. Richness and abundance of steppe birds were low near edges and increased to much higher values in landscapes with larger arable patches. As for ground-nesting birds, abundance was higher in less fragmented landscapes irrespective of distance from edges. This research further supported the observations that the richest bird assemblages in farmland landscapes are found where agricultural habitats are interspersed with wooded habitats (Moreira *et al.* 2005). Sánchez-Oliver *et al.* (2013) revealed a contrast of variables between winter and breeding seasons, with a prominent role of local habitat variables for species density in the first and a more balanced importance of landscape characteristics around plantations and local habitat in the latter. Consequences of afforestation in Mediterranean open farmland are shown through both fragmentation and edge effects of the forest plantations, which seem to increase local bird diversity at the expense of negative effects of steppe birds of European conservation concern (Burfield & van Bommel 2005; Reino *et al.* 2009).

Impacts are even more severe when woodland restoration is practiced using small, highly fragmented pine plantations in a place where matrix is dominated by agricultural habitats and the local natural forests of the region do not belong to the coniferous

vegetation domain. In this case, avian diversity is not enhanced, even with forest development (Carrascal *et al.* 2014) since forest specialists of Mediterranean coniferous forest require larger woodland patches (Santos *et al.* 2006) and an impoverished European forest avifauna, dominated by species of early successional stages, probably contributes to the limits of potential colonization of pure coniferous woodland species (Sánchez-Oliver *et al.* 2013).

Most agricultural policies appear to be applied as if they were to bring about uniform conservation benefits, implicitly assuming that all grassland birds have rather similar or at least compatible habitat requirements and this is simply not true (see Reino *et al.* 2010b). They might be favourable for some species of conservation concern (such as Thekla lark and Corn bunting) in the Iberian cereal-steppes, but detrimental to many others (such as the Little bustard [*Tetrax tetrax*] or the aforementioned Calandra lark), associated with much less fragmented landscapes (Gooch *et al.* 2015).

1.4. The role of Nest Predation

Concept and causes

Predation is one of the most important selective pressures in nature, shaping evolutionary relationships in many systems including that of birds. All birds' life is characterized by a pivotal stage in which they are bound to a particular location on which selective pressures act to modulate their biology and life traits to a large extent, the nest (Ibáñez-Álamo *et al.* 2015).

There is evidence that increased nest-predation processes could rival land-use change as a causal agent in farmland population declines, heightening extinction risk on groups such as passerines (Evans 2004; Beja *et al.* 2014; Ekanayake *et al.* 2015; Lyons *et al.* 2015).

In such cases, more predators do not necessarily mean lower breeding success and nest survival might even remain stable after an increase on predator densities over the years (see Beja *et al.* 2014; Kentie *et al.* 2015). However, loss of nest contents and adults to predators should eventually lead to population declines of vulnerable species and even non-lethal effects could lead birds to avoid breeding or foraging near wooded edges and small patches (Fletcher *et al.* 2010).

Ground-nesting birds seem to be particularly vulnerable to processes of agricultural intensification such as mowing, which increases nest detectability, or the resulting homogeneous vegetation leading to less conspicuous nests (Yanes & Suarez 1996;

Evans 2004; Kentie *et al.* 2015). Indeed, intensification results in higher predator abundance (Pita *et al.* 2009), which in turn can depress bird breeding success and population sizes (Fletcher *et al.* 2010; Beja *et al.* 2014). However, predation rates are also influenced by the composition and configuration of non-agricultural habitats such as those occurring by afforestation (Reino *et al.* 2010a). Forest plantations influence nest predation, for instance, by offering refuges for predators that would be absent or less abundant in open country, but take advantage of these circumstances since some of them are able to nest in tall trees while feeding in adjacent open farmland (Santos *et al.* 2006; Reino *et al.* 2010a). It seems that predation rates are subject to a marked influence of landscape context (Reino *et al.* 2010a) and nest predation might be more dependent on landscape composition and configuration than predator abundances or edge effects *per se* (Donovan *et al.* 1997; Batary & Baldi 2004).

Influence of landscape context on nest predators

Nest predators as a group vary tremendously in habitat use and landscape predictors alone are not enough to effectively assess their composition as a community, since local-scale processes as well as previously mentioned life-traits are known to influence nest predation patterns (Donovan *et al.* 1997). In fact, the relevance of a single predator can vary among habitats and temporarily across the breeding season (Sánchez-Oliver *et al.* 2014; Kentie *et al.* 2015) and different nest predators respond differently to habitat change (reviewed in Ibáñez-Álamo *et al.* 2015). Despite this, they generally have a significantly higher influence on nest predation than edge effects (Reino *et al.* 2010a).

As previously mentioned, forest plantations influence both predator and prey abundances in the surrounding farmland, including generalist predators such as corvids and carnivores, though the amplitude of this effect is influenced by forest characteristics and maturity (Batary & Baldi 2004; Reino *et al.* 2010a). For instance, an increasing cover by eucalyptus plantations ultimately lead to a decline in Red fox (*Vulpes vulpes*) abundance in landscapes dominated by this tree, since lagomorphs and other prey tend to be scarce in more mature forests, reverting the initial positive effect that afforestation has on lagomorph abundance in the early stages of development (Reino *et al.* 2010a). In turn, few were the carnivore species recorded in landscapes dominated by large arable patches and little cover by semi-natural habitats such as cork oak woodlands and Mediterranean forest with shrubland patches. Instead, abundances of carnivores such as these showed a peak in landscape with intermediate size of open farmland patches, something likely justified by this environment of a

mosaic landscape being ideal in providing a combination of secure shelter within woody habitats and food resources at the edges and adjacent open land only available in these human-dominated landscapes (Santos *et al.* 2006; Pita *et al.* 2009).

Other factors influencing nest predation risk

Nest exposure to predators can be influenced by several other factors, such as grazing , which plays a prominent role since it affects sward height and structure, thus modifying exposure (van der Wal & Palmer 2008; Huhta *et al.* 2015) as well as early mowing, which may sometimes lead to nest destruction when not protected (Kentie *et al.* 2015). Another example is the usual low vegetation cover and lack of tree cover typical of clear-cuts which make nests more visible and thus contribute to higher predation rates (Huhta *et al.* 2015). Moreover, nests suffer from the additional risk of livestock trampling in these intensively explored farmlands, which may further reduce breeding success (Reino *et al.* 2010b; Beja *et al.* 2014).

Game management is another factor influencing local small game predators that might also be responsible for nest predation. Predator control is a practice aimed at reducing predation on game species and it should benefit other species, including ground-nesting birds since controlled carnivore species frequently prey on nest (Caro *et al.* 2015). Unfortunately certain specific measures, such as those applied in Mediterranean farmlands seem to be largely ineffective in reducing the abundance of legally controlled predators in all but the most intensively managed game estates (Beja *et al.* 2009) since they indirectly contributed to creating areas of high small game abundance, which should be attractive foraging grounds for a range of predators.

Predator and prey adaptability and coevolution

Risk of depredation is dependent on factors such as nest defense, diversity and abundance of egg predators, as well as the type of cues predators use when finding nests and the ability of placement and concealment by preys (Ekanayake *et al.* 2015). Different types of predators worldwide use different cues to find nests and eggs and predate them, some of which are predator-specific (Stirnemann *et al.* 2015). For instance, mammalian predators such as foxes or rodents use both olfactory and visual cues and forage either diurnally or nocturnally (Price & Banks 2012). As for avian predators, they predominantly use visual cues and forage during daytime (Ekanayake *et al.* 2015).

Conspicuousness of the incubating adult also plays a part in nest predation,

especially when referring to ground-nesting birds since they lack the natural protection from predators that cavity or burrow-nesting species have (Fletcher *et al.* 2010). In addition, some corvids have been documented to strategically aggregate and intensify predation on seasonal or temporal increases in abundance of prey, supplementing their diets with anthropogenic food sources when eggs are not available (Marzluff & Neatherlin 2006; Ekanayake *et al.* 2015).

However, avian prey also possesses anti-predator strategies derived from years of coevolution and selective pressure, in order to reduce nest predation risk. For instance, birds can respond to the presence of predators by altering settlement decisions (Fontaine & Martin 2006), incorporate acoustic cues from different predators and respond accordingly (Hua *et al.* 2014) and also use olfactory and light reflection cues to protect against non-vocal or nocturnal predators (Ibáñez-Álamo *et al.* 2015). Some species are known to nest near protector species, an association sometimes entailing reciprocal protective relationships (Quinn & Ueta 2008). At a physiological level, there are several studies revealing hormonal changes related with nest predation (Travers *et al.* 2010; Fontaine *et al.* 2011; Ibáñez-Álamo *et al.* 2011), which might indirectly affect offspring physiology by altering egg composition as well as incubation and brooding patterns. This in turn may lead to development of phenotypic traits that influence embryo and nestling development (Ibáñez-Álamo *et al.* 2015). However, this may not always be beneficial. An evolution of faster growth, which is to be expected from increased nest predation risk, is thought to create physiological costs that lead to greater adult mortality and shorter life (Metcalfe & Monaghan 2003).

Mediterranean Farmland and the importance of predator identification

Reino *et al.* (2010a) found that it was not the high abundance of lagomorphs and putative nest predators, as well as edges that affected predation on artificial nests so much as landscape context did in the Mediterranean Farmland. This is likely because predation of nests is largely incidental, generally occurring opportunistically when predators are looking for other prey, which should reflect on foraging being a more prevalent factor than predator abundance *per se* (Vickery *et al.* 1992). The patterns shown seem to reflect the range of foraging behaviour of edge predators typically registered in these grasslands, such as red foxes, White storks (*Ciconia ciconia*) and Montagu's harriers (*Circus pygargus*). However, several other species of predators not able to be accounted for could have influence the obtained results. For instance, Beja

et al. (2014) found, in the coastal plateaus of southwestern Portugal, nest predation rates to be much less connected to landscape-level effects or edges. The authors found predator abundances to be the main influences of nest predation in this case, hypothesizing on the much wider gradient of habitat fragmentation that other studies covered in relation to this one, as well as differences in predator communities, thus emphasizing the need to identify the main nest predators in Mediterranean farmland (Beja *et al.* 2014; Ekanayake *et al.* 2015). In fact, when only a few species are responsible for nest failure a strong relationship between environmental factors might indeed occur. However, when predator communities are diverse, a common feature of grasslands, nest loss can be difficult to elucidate on environmental features alone since predator behaviour differs among species or groups of predators (Pita *et al.* 2009; Reino *et al.* 2010a; Lyons *et al.* 2015).

While this is logistically challenging, characterizing the role of predator identity in the relationship between nest predation, habitat characteristics and management is a critical step in studies of nest predation in human altered environments, for it is bound to pay large dividends in terms of understanding nest predation risk and selective pressures influencing parental and offspring antipredator strategies, thus allowing for optimized conservation measures (Cox *et al.* 2012; Ibáñez-Álamo *et al.* 2015; Lyons *et al.* 2015).

1.5. Aims

In this study we aim to address some of the unsolved issues on nest predation in the Mediterranean farmlands. Our main objective was to experimentally evaluate which are some of the main defining environmental variables that influence nest predation, focusing on the presence of interactions between nest predation rates, local vegetation characteristics, landscape attributes and edge distance, while also trying to interpret the relationship between these features and habitat fragmentation. Furthermore, we use camera trapping in order to identify nest predator species and understand a bit more about their role and contribution to general nest predation patterns.

2. Methods

2.1. Study Area

The study was conducted in Southern Portugal, located in the Meso-Mediterranean bioclimatic stage (Moreira 1999), mostly contained within the Special Protection Area (SPA) of Castro Verde (85,000 ha) (**Figure 1**) designated as such under European Directive 79/409/EEC to protect grassland birds. In this area, the landscape is generally flat or gently undulating (100-300 m.a.s.l) and dominated by an agricultural mosaic of cereal, fallow and ploughed fields, created by rotational dry cereal cultivation with annual (*e.g.,* barley and wheat) and permanent crops (*e.g.,* olive groves and vineyards). The climate is Mediterranean, with mild winters (averaging 9°C [5-14°C] in January) and hot summers (24 °C [16-32°C] in July) and >75% of annual rainfall (500-600 mm) concentrated in the months of October through March. From north to south there is a gradient of intensification-abandonment, associated with spatial variation in soil productivity. Tree cover was, until recently, largely restricted to some eucalyptus plantations (*Eucalyptus* sp.) usually 40-60 years old and open holm oak (*Quercus rotundifolia*) woodlands grazed by live stock (mainly cattle and sheep, but also horses and pigs). Since the early 1990s, scrub encroachment and afforestation of umbrella pines (*Pinus pinea*) and holm and cork oaks (*Q. rotundifolia; Quercus suber*) has increased in the periphery of the SPA, mostly due to EU subsidies (Reino *et al.* 2010a).

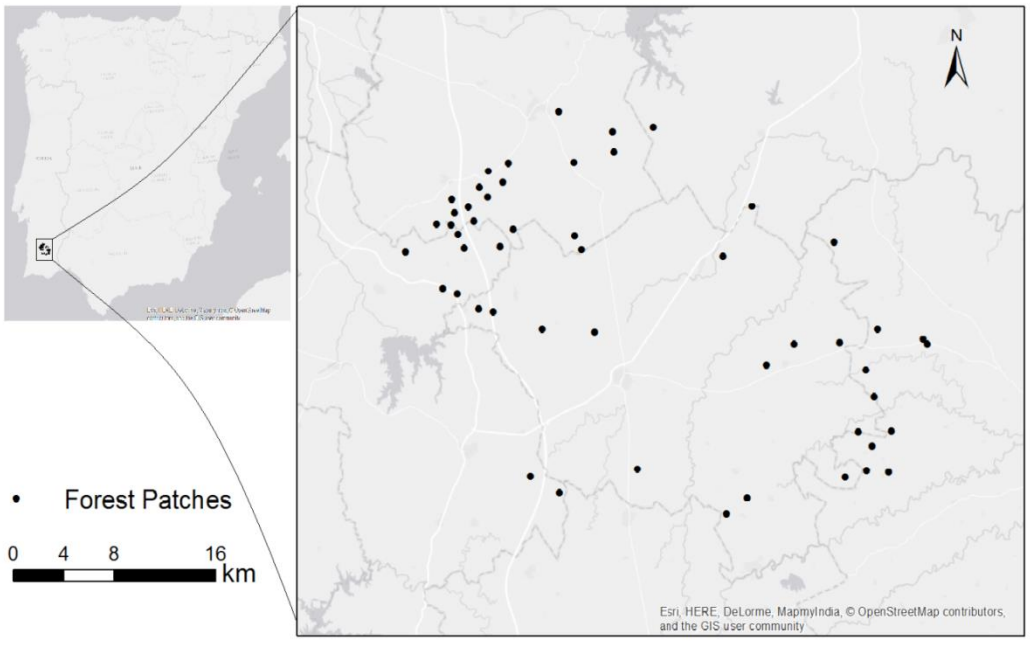

Figure 1. Study Area on Southern Portugal, mostly within the SPA of Castro Verde. Forest patches in the predation experiment are marked as black dots.

Mediterranean farmland bird species

Several steppe bird species are present in the Special Protected Area (SPA) of Castro Verde, including Great bustard (*Otis tarda*), Little bustard, Calandra lark, Lesser kestrel (*Falco naumanni*), Stone curlew (*Burhinus oedicnemus*), Roller (*Coracias garrulus*) and Black-bellied sandgrouse (*Pterocles orientalis*) (Costa *et al.* 2003). This area is of great importance to this group of birds since it comprises, for instance, over 80% of the Portuguese population of Great Bustards, 60% of that for Calandra Lark and *ca.* 20% for others, with a frequency of occurrence throughout all the region of *ca*. 30%. Other ground-nesting species in the area are Fan-tailed warbler (*Cisticola juncidis*), Tawny pipit (*Anthus campestris*), Short-toed lark (*Calandrella brachydactyla*), Crested and Thekla larks, Black-eared wheatear (*Oenanthe hispanica*) and finally Corn bunting, which is a species of conservation concern (Reino *et al.* 2010b) that is also extremely prevalent, occurring in almost 80% of the points (Moreira *et al.* 2007; Beja *et al.* 2014).

Predators

Some of the potential avian nest predators in the Mediterranean region are also of conservation concern, which might incite dilemmas between conservation of predators and that of prey (Pita *et al.* 2009). Potential predators include White stork, Cattle egret (*Bubulcus ibis*) and corvids such as Carrion crow (*Corvus corone*), Jackdaw (*C. monedula*), Jay (*Garrulus glandarius*) and Magpie (*Pica pica*) (Beja *et al.* 2014; Sánchez-Oliver *et al.* 2014). The latter being powerful documented nest predators and urban exploiters, attracted by humanized habitats and recent tree plantations, known to be more able to capture the attention of exploring predators than mature ones (Sánchez-Oliver *et al.* 2013; Carrascal *et al.* 2014).

As for mammals, the most common nest predators are Egyptian mongoose (*Herpestes ichneumon*), Red fox, Wild boar (*Sus scrofa*) and feral dogs *(Canis familiaris*). Small mammals such as Wood mouse (*Apodemus sylvaticus*) or Garden dormouse (*Eliomys quercinus*) can also be found and are important egg predators (Pita *et al.* 2009; Beja *et al.* 2014).

2.2. Sampling design

Sampling was carried out on agricultural fields along transects perpendicular to the edge of 51 forest patches (**Figure 1**), representative of the most common forest plantations in the region (eucalyptus, pinewood and holm and cork oak stands). The selection of sampling sites was based on the criteria employed by Reino *et al.* (2009), which used 1:25,000 land cover maps from 1990 (http://www.igeo.pt/IGEO/portugues/produtos/inf_cartografica.htm) and was then updated through systematic field checking of new forest stands planted up until 2005. A total of 24 patches from this study were used (17 in 2014 and 7 in 2015) and 27 new patches were then selected accordingly. There were 18 experimental parcels of *Quercus* spp*.,* 15 of *Eucalyptus* sp. and 18 of *Pinus pinea* (**Table 1**)*.* Each forest patch was defined as a discrete tree plantation surrounded by open farmland habitats and it was only selected if it was adjacent to either a fallow field or a pasture at least 600 m long and wide, which allowed for sampling open habitats at distances up to 300 m from the nearest forest edge. Each tree plantation and its adjacent grassland were considered an experimental parcel.

Table 1. Tree plantation types for experimental parcels. Grouped by three different height classes (m).

	Height Classes			
Tree plantations	**Class <1.5 m**	**Class 1.5-5 m**	**Class >5 m**	**Total general**
Eucalyptus		2	13	15
Pinus		18		18
Quercus	2	16		18
Total general	2	36	13	51

2.3. Nest predation experiments

Over the course of two breeding seasons (between April 17th and June 4th, 2014 and April 7th and June 5th, 2015) we used artificial nests to estimate variation in bird nest predation rates and potentially identify them. Each nest was baited with two fresh quail eggs (*Coturnix japonica*). Nests were situated in experimental parcels, each of them adjacent to only one of the aforementioned tree plantations, in order to avoid pseudo-replication.

In each experimental parcel, three nests (one monitored nest and two others for control of different situations) were placed at each 100 m interval across transects perpendicular to the forest-grassland edge until a 300 m distance in grassland and a maximum of 300 m in the interior of the forest area, the latter depending on forest size. Each of the three artificial nests were placed 25 m apart from each other, in a line that was parallel to the edge. Nests were made according to the surrounding environment in order to be as least intrusive as possible (ranging from a small depression on the soil to a nest made with vegetation resources nearby) and maximize the similarity to real nests.

We used 29 automatic camera traps (model Scoutguard SG570-6M) with 32 Gb SD memory cards to monitor each main nest for seven days in order to identify predators and estimate predation rates while also detecting livestock activity. Cameras were set to a medium level of sensitivity and triggered when movement was detected in their field of vision. They were either placed in a metal bracket (approximately of 200 mm) nailed to the ground or attached to trees at a comfortable distance from the nest, and supplied with 6V lead acid batteries which were camouflaged and often conspicuously hidden in order maximize concealment from predators and avoid possible behaviour disturbances (Ekanayake *et al.* 2015). One of the control nests was used to control for the camera effect and the other to control for all herbaceous vegetation removal that was occasionally needed for similar levels of nest detection and mainly for the use of artificial nests, which are known to cause potential over or underestimations of predator-related estimates (Batary & Baldi 2004; Beja *et al.* 2014). Extreme care was taken to ensure that predators did not follow us and cameras or nests were never placed when predators were in the general vicinity. Furthermore, trampling of the vegetation around the nests was avoided and research materials were never placed on the ground close to the nests. All of this was performed by the same experienced researchers who performed all tasks using rubber gloves and boots to minimize potential human scent influence (Whelan *et al.* 1994). All nests were checked only once to reduce observer effects and preserve nest concealment (Reino *et al.* 2010a; Ekanayake *et al.* 2015).

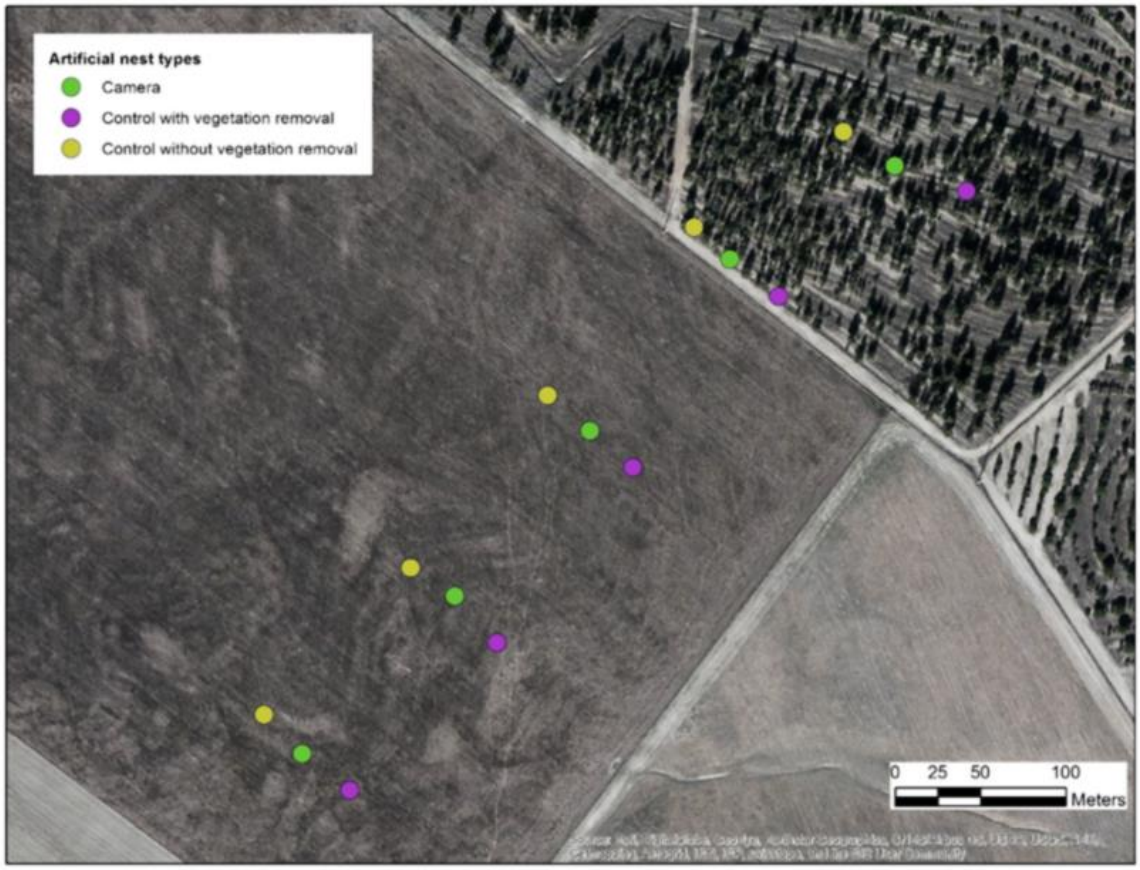

Figure 2. Detailed description of different types of artificial nests placed on the field. Transect is transversal to the edge and each nest type stands 25 m apart from one another, parallel to the edge.

For the first 10 parcels surveyed in 2014, we did not use control nests, thus, we made 276 artificial nests with camera and 222 nests for each control situation, for a total of 720 artificial nests (**Table 2**).

Table 2. Distribution of nests placed in our experiment by Treatment and Nest type.

Treatment	Artificial Nests		Nest Type
Camera	276	498	Manipulated Nests
Control w/ Camera	222		
Control w/ Vegetation	222	222	Non-manipulated Nests
Total general	720	720	

2.4. Local habitat and landscape features

Variation in nest predation rates estimated from the artificial nest experiment was related to different sets of variables reflecting field management, landscape context and predator abundances which were selected based on previous studies that documented the main factors influencing ground nest survival (van der Wal & Palmer 2008; Beja *et al.* 2014).

We characterized each nest location by vegetation height and percentage cover of herbs and bare soil, since these characteristics are known to potentially reduce visual or olfactory cues, diminish predator search efficiency and their composition may be linked to the preferred habitat of some potential nest predators (Duggan *et al.* 2011; Lyons *et al.* 2015). Also characterized were the distance of nests to the closer edge and measured the height and density of trees, of which taller and denser ones reflect higher contrast between edges and adjacent agricultural land (Ries *et al.* 2004).

Landscape was also characterized in order to reflect forest plantation characteristics as well as landscape context (Reino *et al.* 2009)**.** To obtain estimates of landscape context we used 1 km radius circles for all parcels defined from each central point located at the forest edge. This radius is usually defined as such (*e.g*. Reino *et al.* 2009, 2010a; Beja *et al.* 2014) since it is large enough to encompass different land uses despite the relative homogeneity of the landscape, while still remaining within a scale-range to which farmland birds are responsive (Reino *et al.* 2010b). Using a Geographic Information System (GIS) software, together with information collected from field survey, we developed a landscape composition map based on several different types of land use based on the “Carta de Uso e Ocupação do Solo de Portugal Continental para 2007" [COS2007] (Direção-Geral do Território) which possesses the highest level of detail with a total of 193 different classes. Further refinement was then performed to better suite our study area and data analysis, resulting in a total of 11 dominant land-uses (**Table 3**).

From there, we were able to measure the proportions of land occupied by the different plantation types, distances of nest sites to either tree plantations or individual trees or to other sites or linear structures which were considered to be potentially able to affect habitat use by predators or predation in some way, such as: individual trees in open farmland; industrial or housing facilities; paved roads; irrigation channels, water lines and arboreal and shrubby windbreaks (Pita *et al.* 2009; Sánchez-Oliver *et al.* 2013; Lyons *et al.* 2015).

In order to estimate habitat fragmentation we computed several landscape metrics

using Patch Analyst extension of ArcGIS 10.1 (version 5.1) (Rempel *et al.* 2012) including mean patch size, land-use heterogeneity, edge density and the area-weighted mean shape index (AWMSI) for each patch surveyed. The latter is a measure of shape complexity, averaging perimeter-to-area ration for a given previously defined class weighted by the size of its patches (Rempel *et al.* 2012). It essentially conveys the extent to which patch shapes deviates from circularity, thus reflecting increases in patch complexity and consequently in edge-affected habitats.

Table 3. Dominant land-uses and percentage of parcels with occurrence in the 51 studied patches (%).

Dominant land-uses	Presence in study patches (%)
Annual crops and pastures	100
Building/Urban/Industrial	80.4
Infrastructures	70.6
Isolated Trees	86.3
Open woodland	98.0
Permanent crops	52.9
Shrubland	76.5
Streams and artificial canals	80.4
Unpaved road	100
Water	94.1
Woodland	70.6

2.5. Statistical Analysis

In order to better understand the potential relationship existing between predation rates and all explanatory variables measured, a Generalized Linear Mixed Model (GLMM) approach was used (Bolker *et al.* 2008). The analysis started by modelling predation probability according to field explanatory variables using a binomial response variable (non-predated = 0; predated = 1) and thus, a binomial error distribution which uses the logit-link function and thereby accounts for potential lack of independence among nests located in each transect (Zuur *et al.* 2009).

Model development started by checking univariate responses of local predictor variables on nest predation rates in order to access if the latter were significantly influenced by each, individually. Variables were then selected to test more complex models with a multivariate response, even if some were not significant, as it is possible for variables' effect to only become perceptible in an interacting multivariate context. An analogous process was also performed for gradients obtained from landscape variables, although it was soon discarded as none revealed influences on nest

predation context. Given the relatively small dataset, only linear ($y = a + bx$), responses were evaluated, to avoid obtaining overly complex models. For each model, scatterplots and regression of residuals diagnostics were used to inspect the shape of the fitted curves and check for eventual problems resulting from outliers and other influential points (Legendre & Legendre 1998).

Further analysis involved a Multimodel Inference (MI) approach, which is a method based on an estimated weighted average across all subset models that takes into account obtained model weights (Burnham & Anderson 2002). The full model was based on the terms selected in the previous univariate approach for inferring relevant variables and interactions between them. In this design, the parcel was treated as a random effect, whereas nest manipulation (non-manipulated = 0; manipulated = 1), vegetation height around nest, presence or absence of Carrion crow and habitat type were all treated as fixed effects terms. In order to avoid unnecessary added noise and complexity in the developed models that occurred mainly due to points associated with edge, we opted to exclude 'edge' level of habitat type, thus obtaining another two leveled predictor (forest and grassland), allowing for more clarity in model design. The null model was simply fitted to the intercept without any of the aforementioned covariates. The subset models included all possible combinations of each variable including the interaction terms between pairs of variables.

Due to potential intercorrelations among variables, the use of model-averaged regular regression coefficients (Burnham & Anderson 2002) to assess the relative contribution of individual variables to nest predation frequency in the context of our *a priori* models was invalid (Cade 2015). Instead, we computed model averaging for the partial standardized coefficients obtained by multiplying the unstandardized coefficient in the model (β_i) by the partial standard deviation of the variable (s^*_{xi}): $\beta_i^* = \beta_i \, s^*_{xi}$ (Bring 1994), where $s^*_{xi} =$, s_i is the standard deviation of the variable in the sample, n is the sample size, k is the number of variables in the model, and VIF_i, is the variance inflation factor of the variable (Cade 2015). Then, we estimated the relative importance of each variable within each model as the ratio of its partial standardized regression coefficient to the largest partial standardized regression coefficient (absolute value) in the model (Cade 2015). Unconditional standard errors of estimates were used to evaluate the precision of model average estimates, with a 95% confidence interval (CI). Estimates whose confidence limits included zero were viewed as having equivocal meaning (Burnham & Anderson 2002).

All analyses were performed using R 3.2.5 software (R Development Core Team 2016). GLMM models were developed using glmer function from the 'lme4' package

(Douglas *et al.* 2016) and model averaging from MI was performed using model.avg, partial.sd and dredge functions from 'MuMIn' package (Bartoń 2016).

3. Results

3.1. Experimental parcel characteristics

The mean vegetation height surrounding nests was significantly different for each habitat ($F_{2.717}$ = 39.4027, p < 0.0001), being higher in open grassland habitat (21.48 ± 1.14 cm) and lower in woodlands (11.47 ± 0.65 cm). This tendency remains similar for all three nest types (all interactions of mean height with each experiment type were significant with p < 0.0001, see **Figure 3**), as well as for manipulated and non-manipulated nests ($F_{2.219}$ = 10.067, p < 0.0001; $F_{2.495}$ = 33.0185, p < 0.0001, respectively).

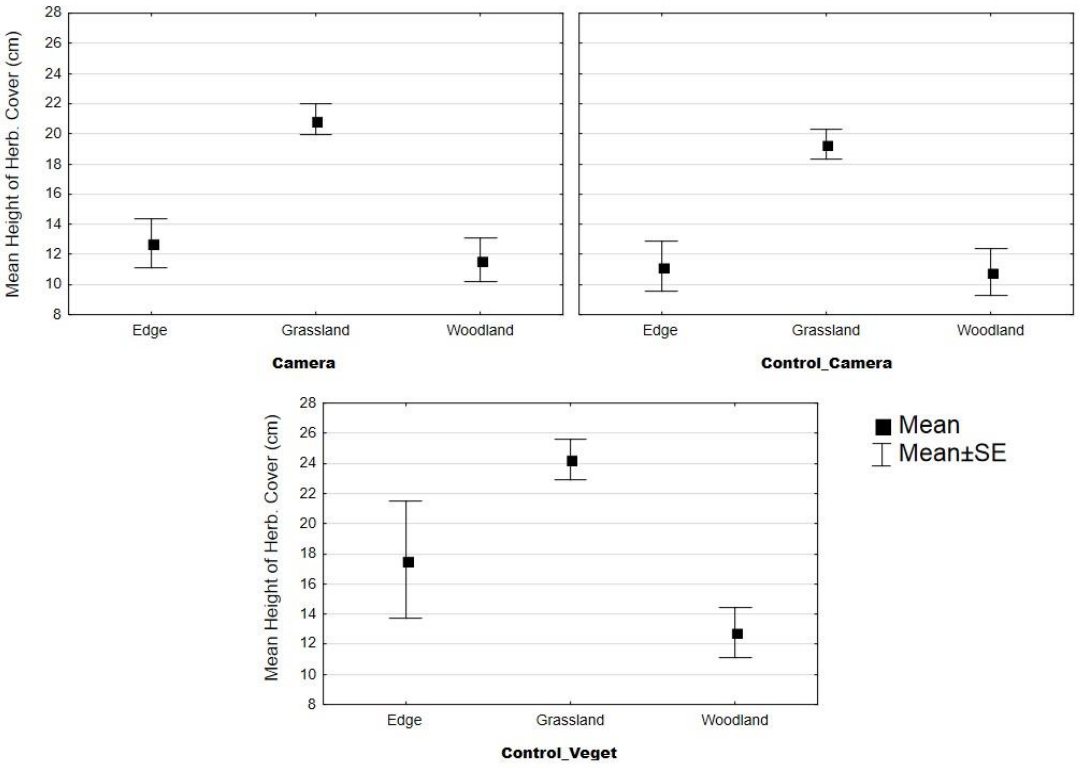

Figure 3. Mean height of nest herbaceous cover (cm) in the three different habitats (Edge, Grassland and Woodland) per nest treatment type.

3.2. Predation experiment

Nest predation rates

We classified nests as predated if eggs were missing or damaged, except when there was evidence of ploughing or livestock trampling, in which case they were not considered as such and were simply excluded from further analyses (Beja *et al.* 2014). Trampling was assessed from the presence of either hoof marks or smashed eggs, with no apparent signs of predator consumption. Images obtained by camera traps for each parcel were also thoroughly verified for conclusive information regarding nest fate. Multiple visits post-predation by the same species of predator to the same nest were only counted once for each analysis as it may have been the same individual.

Eight controls were not found and there was one nest with missing data due to camera malfunction. Thirty nests were trampled or ploughed and six more were eliminated from analysis for different reasons. Taking into account these limitations, data analysis considered 328 (48.6%) predated nests and 347 not predated (51.4%).

Our results revealed a higher nest predation frequency in experimental parcels with *Pinus* tree plantations (52.6%) and considerably lower in *Quercus* tree plantations (43.1%), while *Eucalyptus* stands revealed intermediate values (49.2%; **Table 4**). However, differences between different habitats (i.e. woodland, edge and grassland) were not significant ($F_{2.672} = 0.5528$, $p = 0.5756$, see **Figure 4** and **5**).

Considering nest distance to the nearest edge of forest stands in each parcel, predation occurred more frequently at 200 m from the edge towards woodland (60.5%), followed by nests placed nearer the edge (52.8%). Predation frequency with the lowest value was at 100 m from the edge in forest habitats (woodland) (43.3%) with frequencies below 50% in all other distances from edge in open-land habitats (grassland) (**Table 4, Figure 5**). Overall, our results did not show a significant correlation between nest predation and distance to forest edge (**Figure 6a**). However, a significant correlation between distances of nests to the nearest edge of *Eucalyptus* stands was found (**Figure 6b**).

Table 4. Absolute and relative values of predation for each tree plantation type.

Tree plantations	Predated Nests	Total Nests	% Predated Nests
Eucalyptus	93	189	49.2
Pinus	142	270	52.6
Quercus	93	216	43.1
Total general	328	675	48.6

Table 5. Number of Predated nests and Predated nest frequency according to distance to Edge (towards Grassland and Woodland).

	Distances (m)	Non-Predated Nests	Predated Nests	% Predated Nests
Woodland	-300	8	10	55.6
	-200	15	23	**60.5**
	-100	72	55	43.3
Edge	0	60	67	52.8
Grassland	100	68	54	44.3
	200	64	60	48.4
	300	60	59	49.6
Total general		347	328	48.6

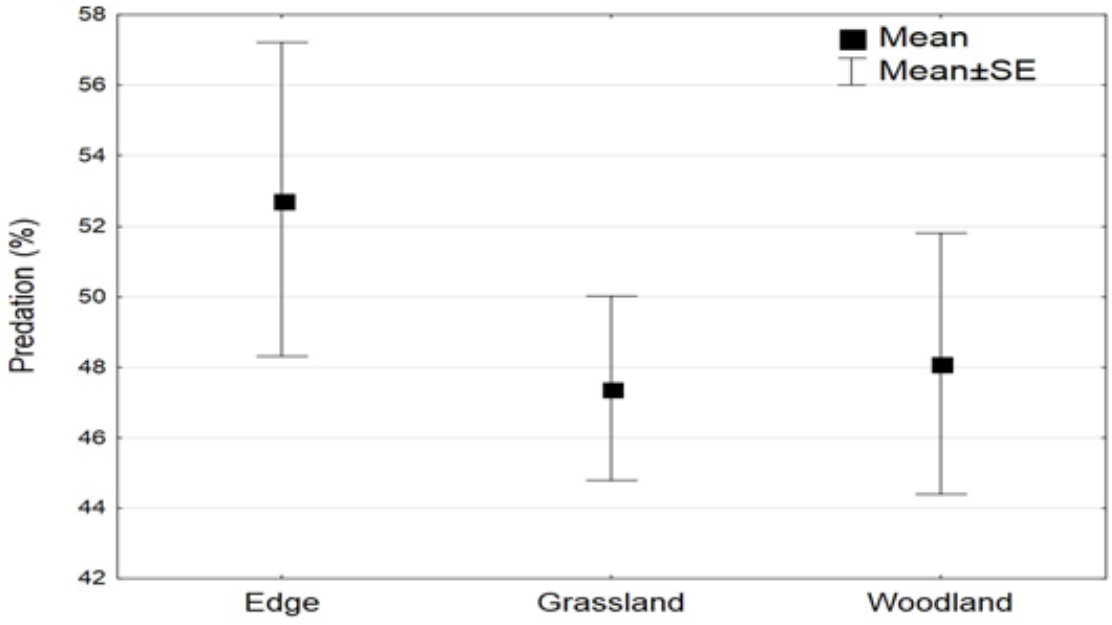

Figure 4. Average Predation (%) in the three different Habitat types (Edge, Grassland and Woodland), showing no significance ($F_{2.672} = 0.5528$, $p = 0.5756$).

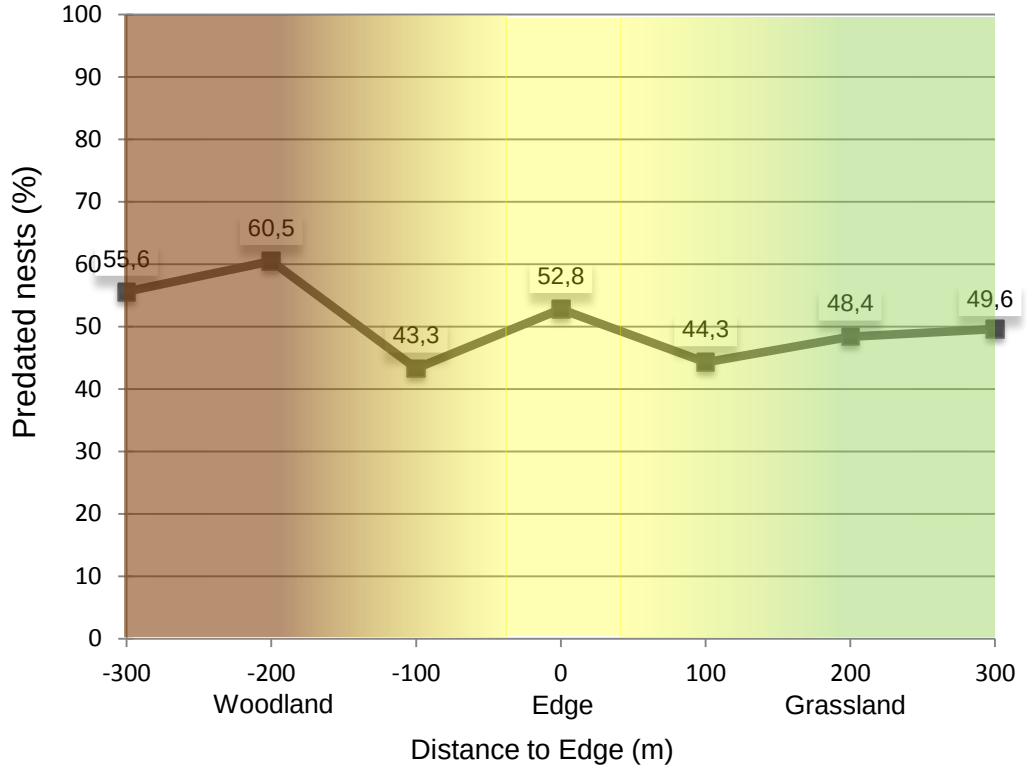

Figure 5. Graphical representation of predated nests (%) across the landscape with woodland and grassland represented by their distances to edge.

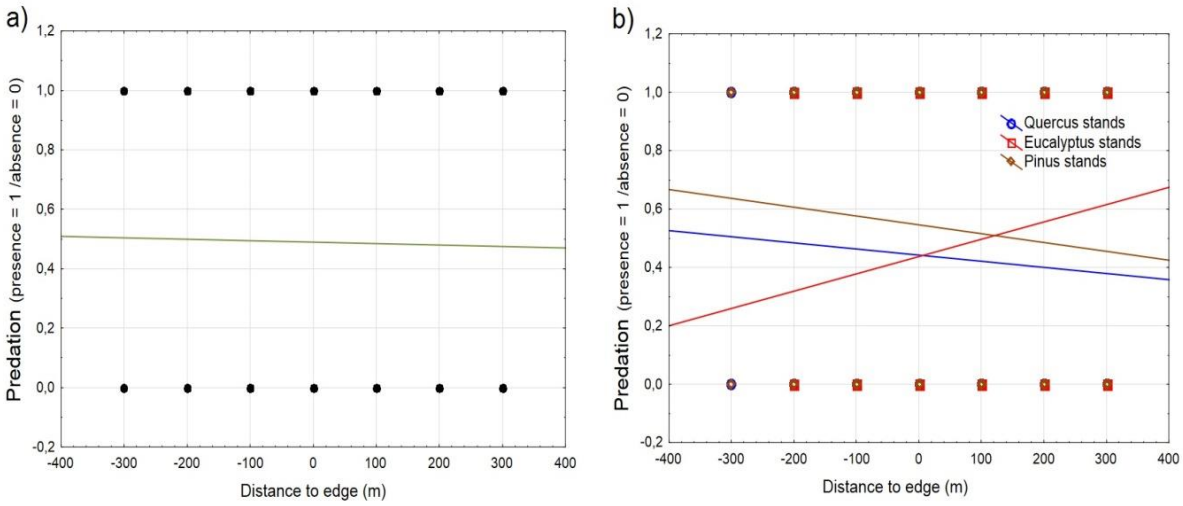

Figure 6. Pearson Correlation coefficient tests between Nest predation and Distance to edges, overall in **a)** (overall: r^2 = 0.0002; p = 0.6933, green line) and for each habitat type in **b)** (*Quercus* stands: r^2 = 0.0052, p = 0.2911, blue line; *Eucalyptus* stands: r^2 = 0.0313, p > 0.05, red line; *Pinus* stands: r^2 = 0.0100, p = 0.1006, brown line).

Furthermore, nests were predated significantly more frequently ($F_{2.672}$ = 3.999, p < 0.05) in the Camera control treatment (55.9%) when compared with nests under Vegetation Control treatment (42.2%, **Table 6,** see also **Figure 7**). However, when accounting for potential differences among different habitats, significant effects were not found (Camera experiment: $F_{2.253}$ = 0.8295, p = 0.4374; Camera control: $F_{2.210}$ = 0.2, p = 0.8189; Vegetation control: $F_{2.203}$ = 1.7754, p = 0.1720; **Figure 8**).

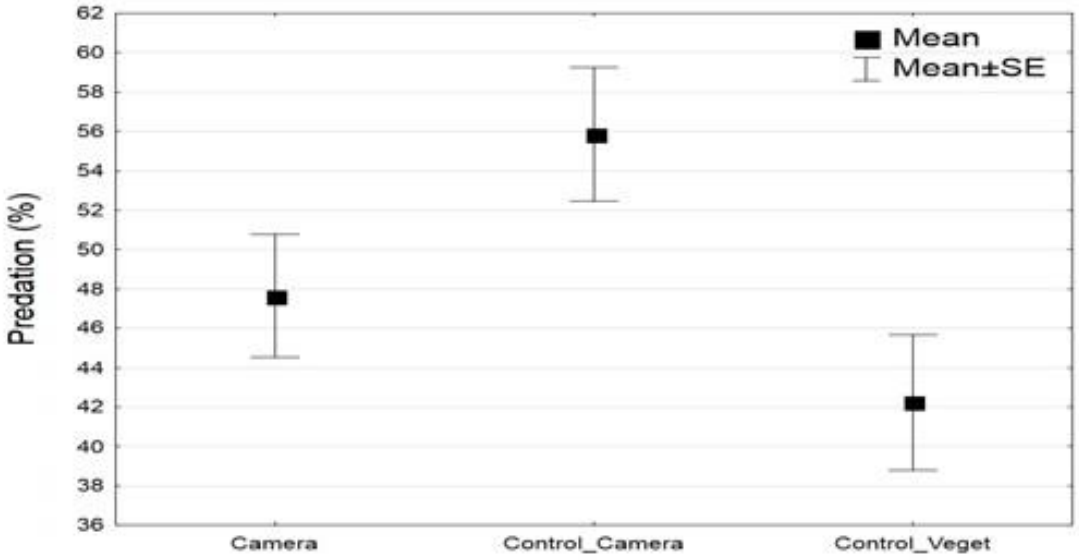

Figure 7. Average nest predation (%) for each experiment type and respective significance: Camera, Control for camera and Control for vegetation.

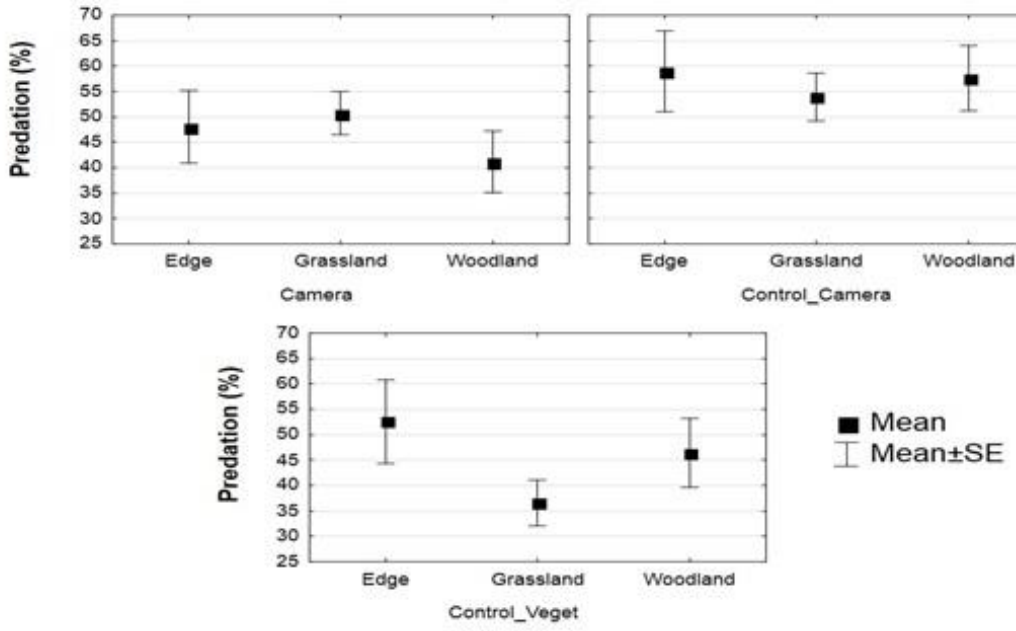

Figure 8. Average nest predation (%) for the three types of experiment: with camera: $F_{2.253}$ = 0.8295, p = 0.4374; control for camera: $F_{2.210}$ = 0.2, p = 0.8189; and control for vegetation: $F_{2.203}$ = 1.7754, p = 0.1720. Experiments are compared with three different levels of habitat (edge, grassland and woodland).

Overall, manipulated nests were significantly more predated than non-manipulated ones ($F_{1.673}$ = 4.8203, p < 0.05). Specifically, manipulated nests in the Grassland were more frequently predated than non-manipulated ones ($F_{1.363}$ = 7.6624, p < 0.05) but not in both edge and woodland habitats (**Figure 9**).

However, there were no significant differences among general levels of habitat type for either non-manipulated ($F_{2.204}$ = 1.7754, p = 0.1720) or manipulated nests ($F_{2.466}$ = 0.2338, p = 0.7916).

Table 6. Number of predated nests and predation frequency by treatment type.

Nest Type	Non-predated Nests	Predated Nests	% Predated Nests
Camera	134	122	47.7
Camera Control	94	119	55.9
Vegetation Control	119	87	42.2
Total general	347	328	48.6

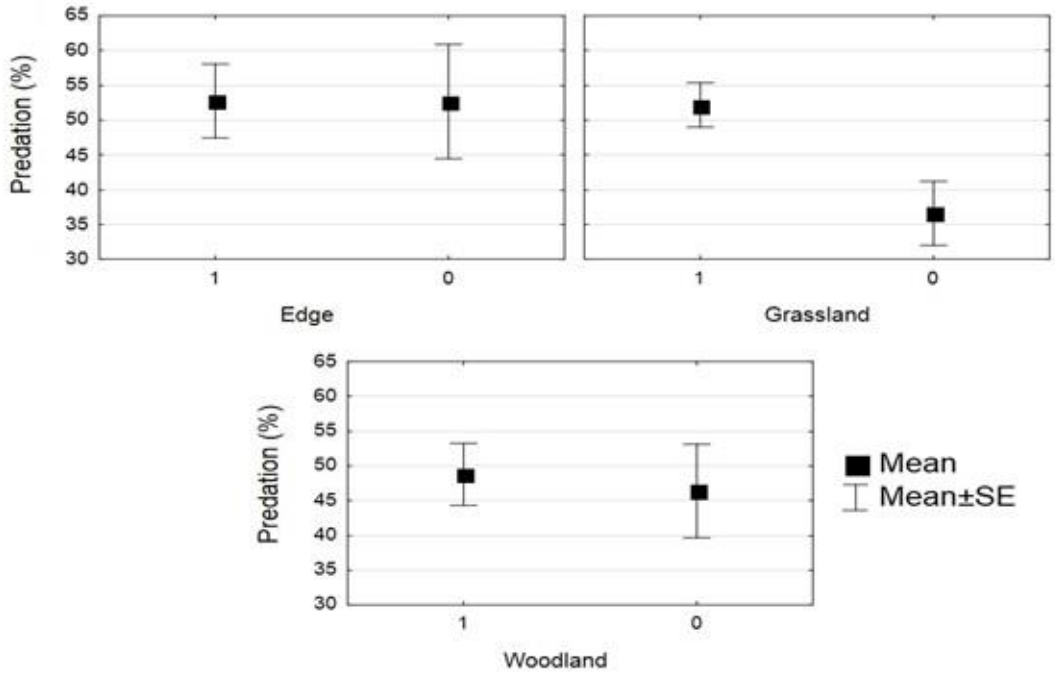

Figure 9. Difference of mean nest predation (%) between manipulated (1) and non-manipulated nests (0) for each habitat type (edge, grassland and woodland). Significant differences only shown for Grassland ($F_{1.363}$ = 7.6624, p < 0.05. Edge and Woodland were both non-significant ($F_{1.125}$ = 0.0003, p = 0.9855 and $F_{1.181}$ = 0.088, p = 0.7670, respectively).

Predator species

We identified 17 different species of predators among 89 nests of the 328 predated nests (**Table 7**). Carrion crow (*Corvus corone*) was the main predator on artificial nests with camera, accounting for almost half of the predated nests that were identified (42.62%). Overall, corvids were identified as predators of more than half of predated nests (50.8%). Nonetheless it was not possible to confidently identify species for a total of 34 nests, representing 27.85% of predation events successfully detected by cameras (although Eurasian jay (*Garrulus glandarius*) is likely to be one of the predators in these events).

Table 7. Description of all species of predators found and corresponding number of nests predated by them. Highlighted are *Corvus corone* and Unknown species which constitute the great majority of predators found.

Predator Species	Predator Species (common names)	Number of Nests	% Nests Predated
Buteo buteo	Common buzzard	1	0.82
Circus pygargus	Montagu's harrier	8	6.56
Corvus corax	Common raven	4	3.28
Corvus corone	**Carrion crow**	**52**	**42.62**
Corvus corone/Circus pygargus	Carrion crow/Montagu's harrier	1	0.82
Cow		4	3.28
Cyanopica cyanus	Azure-winged magpie	2	1.64
Eliomys quercinus	Garden dormouse	4	3.28
Herpestes ichneumon	Egyptian mongoose	2	1.64
Lepus granatensis	Iberian hare	1	0.82
Otis tarda	Great bustard	1	0.82
Pica pica	Magpie	3	2.46
Mouse		1	0.82
Sheep		1	0.82
Sus scrofa	Wild boar	1	0.82
unknown		**33**	**27.03**
unknown/Garrulus glandarius	unknown/Eurasian jay	1	0.82
Vulpes vulpes	Red fox	2	1.64
Total general		122	100

The analysis of potential predation events was made by screening all photos collected in nests with camera traps. This allowed us to estimate the number of days till

a positive predation event, independently of the predator (**Figure 10a**). However, our results did not reveal any pattern associated with a particular species or predation event suggesting some kind of pattern. Yet, the species with a wider range of predation events, *i.e.,* days until a successful predation was the Carrion crow, which is also the commonest species. Several other species, such as Montagu's Harrier, Red fox, cow and Azure-winged magpie (*Cyanopica cyanus*) also showed a great range of days until predation, which may vary from 1 day up to 5 or 6 days. Only the Magpie (*Pica pica*) and the Common raven (*Corvus corax*) showed a more restricted range of time until nest predation (between 2 and 4 days for both species). All other species identified represented only one predation event each. By comparing days until predation for each different habitat (**Figure 10b**), we found that both Carrion crow and the cluster of unknown species showed a more restricted range of time until predation in woodland habitat than in others. Furthermore, for most species, predation in grassland occurred during the first four days of experiment, while in the edge, most events of predation tended to occur generally after the third day, except for Common buzzard (*Buteo buteo*) and Garden dormouse (*Eliomys quercinus*). In woodland, only the Carrion crow exceeded the fifth day until predation once, with all other species falling under the 0 to 5 days range.

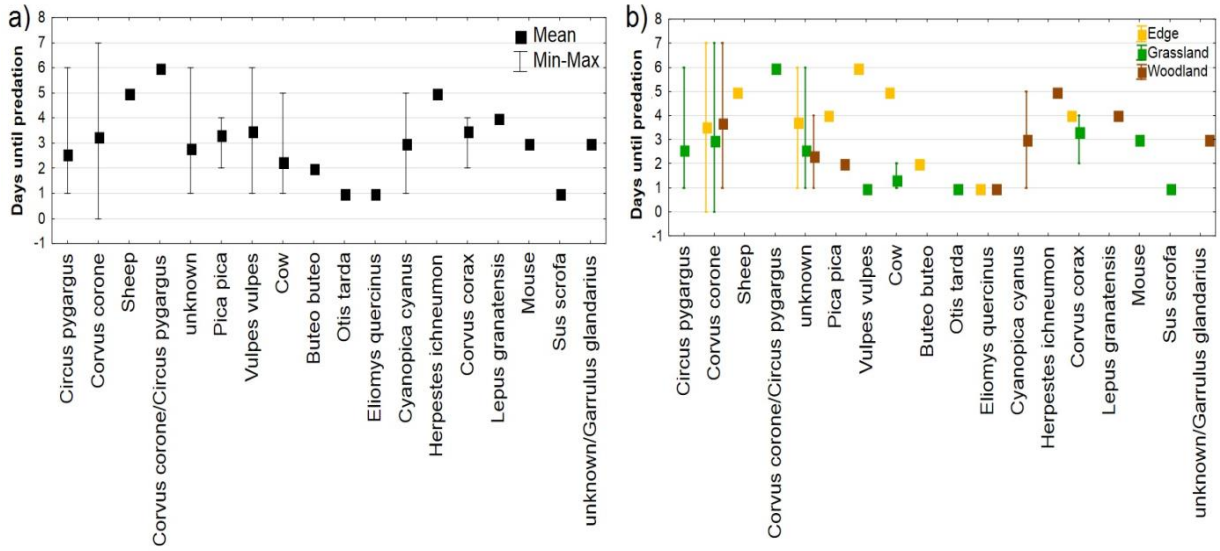

Figure 10. Mean days for nest predation by each predator species identified: in general (**a**) and on each habitat type (**b**). Bars represent least and highest amount of days until predation for each species.

3.3. Predation patterns

Univariate analysis performed using local variables revealed nest manipulation (z = 2.59, $p < 0.05$) and vegetation height (z = -3.21, $p < 0.05$) were both significant in explaining nest predation rates, while presence/absence of Carrion crow (z = -0.002, p = 0.999) and habitat type (z = 1.34, p = 0.51) were not.

Model averaging using the MI approach revealed that the most important supportive variables explaining variation of predation rates were the vegetation height (Importance = 1.00), its interaction with manipulation of nests (Importance = 0.93) and the interaction between grassland and the relative presence of Carrion crow (Importance = 0.72; **Table 8**). This is better illustrated in **Figure 11**, where Predation probability is shown across a gradient of vegetation height in either grassland or forest habitats, highlighting differences registered due to the presence or absence of Carrion crow and nest-site manipulation. Namely, predation probability decreases with increasing vegetation height in both habitat types, an effect that is severely more pronounced when nest-site manipulation is absent. Furthermore, while manipulation effect is relatively similar between both habitat types, Carrion crow presence has higher impact on grassland (**Figure 11a**) than in forest segments (**Figure 11b**) and this effect on nest predation is especially pronounced when there is nest-site manipulation. Curiously, the effect of this species on predation probability appears to be analogous but reversed between different habitat-types (higher predation levels occurred where Carrion crows were absent in forests while the opposite trend was shown in grassland segments).

Table 8. Relative predictor variable estimates and corresponding significance values and relative importance for the model averaging based on the global model which included all possible pairwise interactions between predictors. R^2 = 0.30164.

	Estimate	Std. Error	Importance
Herb. height	-0.43	0.16	1
Nest manip.*Herb. height	0.4	0.12	0.93
Grassland*Carrion crow	0.31	0.15	0.72
Carrion crow	-0.21	0.22	0.48
Nest manip.	-0.12	0.12	0.28
Grassland*Herb. height	-0.1	0.13	0.23
Nest manip.*Carrion crow	0.04	0.11	0.1
Grassland	-0.04	0.1	0.09
Herb. Height*Carrion crow	0.02	0.09	0.05
Grassland*Nest manip.	-0.02	0.07	0.04
Intercept	0	0	0

Another set of models using a gradient of landscape predictors that were obtained from a Principle Component Analysis (PCA; see **Annex i**) was also considered. However, all models revealed Principal Components to be non-significant explanatory variables of nest predation and were therefore discarded from further analysis.

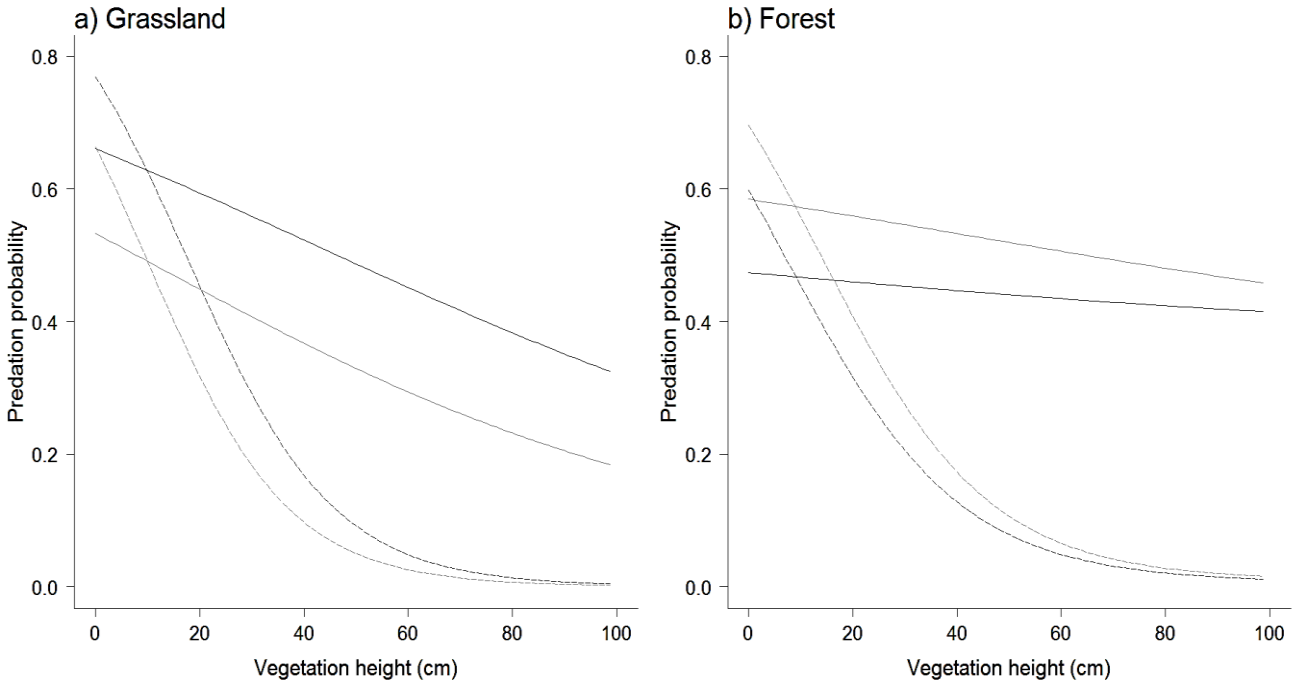

Figure 11. Predation probability according to vegetation height around the nest: in grassland segment of parcel (**a**) and in forest segment (**b**). Full black line represents presence of Carrion crow and nest manipulation; black dashed line represents presence of Carrion crow and no nest manipulation; full grey line represents absence of Carrion crow and occurrence of nest manipulation and dashed grey line represents neither Carrion crow nor manipulation.

4. Discussion

4.1. Observed patterns in experimental parcels

Grazing regimes, local features and habitat fragmentation are thought to be major drivers of grassland bird species densities and distribution in Mediterranean farmland (Reino *et al.* 2010b, 2013).

Vegetation height around nests was always higher in open-grassland than in edge and woodland habitats in our study area, which is a logical result since much of the habitat in the Mediterranean farmland is composed of a large quantity of cereal steppes, resulting mostly of dry cereal crops and pastures (Moreira *et al.* 2007; Pita *et al.* 2009). However, this implies situational mowing which, when occurring, might favor higher nest detectability (Kentie *et al.* 2015).

There is also a great presence of cattle and sheep that can lead to high levels of grazing and trampling rates (Beja *et al.* 2014). This, together with the fact that many of these recent forest stands severely limit the development of ground vegetation, can potentially justify vegetation being lower in woodland habitats (Reino *et al.* 2009, 2010b).

4.2. Driving forces of Nest Predation

Predation of eggs is a major cause of reproductive failure among birds (Ekanayake *et al.* 2015) and has been identified for some species as a key threatening process contributing to a heightened risk of extinction (Peery & Henry 2010). Risk of depredation appears to be dependent on several factors such as nest defense, diversity and abundance of predators and types of cues used by predators to find nests, as well as nest placement and concealment by prey (Ibáñez-Álamo *et al.* 2015).

We were interested in finding what were the main factors influencing predation in the Mediterranean farmlands of Castro Verde while also obtaining some insights on the existing predator community.

The main type of afforestation in the last years was mainly of *Pinus* spp., which appear to impact local biodiversity since they generally have higher tree cover and less structural heterogeneity than natural Mediterranean woodlands (Carrascal *et al.* 2014). In our study, nest predation was indeed more frequent in parcels associated with *Pinus* tree plantations than in any other type of parcel, being the only case were it surpassed 50% of nest predation, overall (**Table 4**). On the other hand *Quercus* stands had their

nests nearly 10% less predated. This seems to strengthen the findings of previous authors, which suggested that generally fragmented pine plantations in a Mediterranean landscape dominated by agricultural habitats are too simplistic in structure to enhance avian diversity or even maintain rich bird communities, mainly due to the lack of suitable microhabitats in the understory (López & Moro 1997). However, Reino *et al.* (2010a) found contradicting results on a similar study area, with higher predation rates found near young oak plantations and lower on adult eucalyptus plantations. Despite this, there is the agreement that afforestation, mainly in areas of conservation concern, may represent serious threats to the survival of ground-nesting birds (Reino *et al.* 2010a).

There is a general evidence pointing towards higher predation rates around edges in grassland habitats (Batary & Baldi 2004; Reino *et al.* 2009), although this pattern is far from being universal (Reino *et al.* 2010a; Beja *et al.* 2014). In this study, we found that, on average, nest predation rates were higher near edges than in grassland or woodland habitats, albeit differences were not significant and rates fluctuated with different distances, actually reaching the highest frequencies in the farthest distances of forest habitat (200 and 300 m of woodland; **Figure 5**). However, this may be the consequence of fewer data existing for those same distances, as previously mentioned (see also **Table 5**). Curiously, both lower values of predation frequency occur at 100 m of the edge (in both woodland and grassland territory) and in this case with equivalent sample sizes. So it seems difficult to attribute predation patterns to edge effects alone. Indeed, edge tendencies seem to favor prediction of bird species assemblages rather than nest predation rates. For instance, in Castro Verde, typical farmland birds were either neutral or responded positively to edge effects while open farmland specialists such as Calandra lark responded negatively (Reino *et al.* 2009).

While edge distance did not seem to be correlated with nest predation overall, such an effect was found for the particular case of eucalyptus stands in which predation decreased towards woodland and increased towards grassland. This seems to reflect the influence of landscape context, so often described as one of the main factors shaping nest predation rates more than edges *per se* (see Donovan *et al.* 1997; Reino *et al.* 2010a; Sánchez-Oliver *et al.* 2014; Caro *et al.* 2015). For instance, Reino *et al.* (2010a) found predation rates to decrease with cover by eucalyptus stands while increasing with cover by young oak plantations. This could be justified by these younger plantations being generally more attractive since newer habitats tend to catch the attention of exploring predators better than older plantations while also being more widely open, thus making artificial nests more visible (Suvorov *et al.*; Reino *et al.*

2010a; Sánchez-Oliver *et al.* 2014).

However, correlations for landscape features were few and not the most relevant in predicting nest predation rates for our study. Indeed, local explanatory variables such as vegetation height around nest, the interaction between nest manipulation and the former and the presence/absence of Carrion crow in a particular habitat type (grassland) were the most important features in terms of predicting nest predation patterns, as suggested by our models (**Table 8**, **Figure 11**). Beja *et al.* (2014) also found field variables such as vegetation height and proportion of bare soil to be particularly important in nest predation. Huhta *et al.* (2015) found that vegetation cover of nests decreased the probability of a nest to be predated, while another study also reported that higher vegetation cover is known to increase predation time, thus resulting in lower rates of nest loss (Lyons *et al.* 2015). Grazing intensity could have also played a part on the alteration of vegetation height (van der Wal & Palmer 2008; Beja *et al.* 2014), particularly in grasslands, which in turn could have increased nest exposure to predators and justify the importance of *C. corone*, by far the most prevalent predator in our study area. Manipulation influence should be analogous to that of vegetation height in the sense that non-manipulated nests simply consisted of laying down the eggs on a small depression of the ground with as little interaction with vegetation around the nest as possible, while manipulated nests had the nearest vegetation removed in order for the camera to be able to correctly detect movements around or in the nest (the same was done for the camera control). From this perspective, the interaction between both variables would make sense when defining nest predation patterns. Despite this, the influence of scent and the human creation of the nest might have also played a role. However, if this was the case, it would make sense for the camera control experiments to have similar predation rates to the camera experiments, which was not the case. Instead we obtained a considerable difference between camera and camera control experiments, slightly larger than that between camera and vegetation control experiments (**Figure 7**, but see more below).

As previously stated, no landscape gradients were significant predictors of nest predation rates. Although there are several differences between results obtained in this study and others, especially when it comes to the influence of landscape context on nest predation rates, several other factors could have influenced this outcome. Firstly, the measured landscape variables and the modeling approach using PCA gradients based on them may not have been sufficiently in depth or it may otherwise have generated confounding effects, thus omitting the effect of isolated variables. A more extensive analysis could potentially reveal new patterns associated with predation

rates. There is, however, the possibility that these factors simply did not affect our study area. For instance, some authors defend that bird nest predation is largely incidental and occur opportunistically when predators are looking for other prey (Vickery *et al.* 1992) which would lead to predation being more related to foraging behaviour than any other factor. Furthermore, the observed patterns may also reflect the operation of predators neither found nor analyzed in our study area (Batary & Baldi 2004; Reino *et al.* 2010a). For instance, the fact that Carrion crow presence in forest type habitats had seemingly reverse effects on predation rates in comparison with grassland habitats may reflect not only the difference in foraging behaviours found in those habitat types, but also their interactions with other potential predator species leading to the alienation of the latter. Considering all this, coupled with it being a medium sized animal which should have more difficulties predating in forest environments could result in an overall lower predation rate even though Carrion crows were present. Thus, understanding the differences in predator composition for each study area is fundamental (Beja *et al.* 2014) and might be a major factor behind the inconsistencies seen between results of different studies.

The use of artificial nests

Artificial nests are the most commonly used ecological indicator of nest predation risk. Although their use may provide inaccurate estimates of real nest predation rates (*e.g.,* Major & Kendal 1996; Stirnemann *et al.* 2015; Patterson *et al.* 2016) and extrapolation of results to real nest rates is to this day much debated (see Major & Kendal 1996; Beja *et al.* 2014), it is generally accepted that they are, for comparative purposes, useful substitutes of real nests, since they ensure flexibility in experimental design and large sample sizes (Batary & Baldi 2004; Reino *et al.* 2010a), while also being reasonably easy and cost-effective (Huhta *et al.* 2015). The use of artificial nests in our experiment made possible the application of a standardized methodology across a variety of habitat types, which is the only way to encompass different species with particular behavioural idiosyncrasies and microhabitat selection patterns (Stirnemann *et al.* 2015). Furthermore, artificial nests were used in previous studies as the only way to obtain consistent estimates of nest predation in habitats that were actively avoided by birds due to high nest failure risk (Latif *et al.* 2012) and they are also useful in identifying factors affecting spatial and temporal variation in nest survival (Batary & Baldi 2004; Beja *et al.* 2014; Sánchez-Oliver *et al.* 2014). However, artificial nests differ from natural ones in a number of important ways which may influence predation rates and predators, such as size, colour and odour of the nests and eggs, artificial selection

of nest site, the lack of an incubating adult and the absence of nestlings (Davison & Bollinger 2000; Huhta *et al.* 2015). Furthermore, artificial nests do not necessarily attract predators at the same frequency as real nests (Major & Kendal 1996; Patterson *et al.* 2016).

For this study, we did not focus on absolute predation rates and were instead more interested in comparative rates across a gradient of local and landscape variables, which falls under the aforementioned criteria of correct use of them. The use of nearby and freshly cut vegetation to assemble the nests as well as protective gloves to avoid leaving human scent should have also contributed to diminish its influence on the variables we were interested on and, although manipulation effects were shown to be significant, this was more likely associated to the manipulation of vegetation around the nests influencing concealment than on the artificial nests *per se*, as previously mentioned. Thus, although one should not presume to draw conclusions on estimates of survival rates of real nests with artificial nests' studies, it was, together with the reduced costs of using camera trap technology, one of the better ways to properly investigate and identify nest predator communities and their spatial patterns (see also Batary & Baldi 2004; Beja *et al.* 2014; Huhta *et al.* 2015; Ibáñez-Álamo *et al.* 2015).

Camera traps and identified predators

Using camera traps for ecological research and management is a growing trend (Meek *et al.* 2016). Although its usage tends to be generally safe for nests (Richardson *et al.* 2009; Ibáñez-Álamo *et al.* 2015; Stirnemann *et al.* 2015), this is not always the case, especially when it concerns abundance studies (Ekanayake *et al.* 2015; Meek *et al.* 2016). Concerns are focused on cameras changing the behaviour of an animal by either attracting or repelling them from a sampling device, which constitutes an interference and should be accounted for in data analysis (Engeman 2005). Despite a significant effort being made on the development of sophisticated analytical methods to analyze data generated by camera traps (see O'brien *et al.* 2011), few recognize the disturbance effect that it may pose. Therefore, validating this assumption in specific studies is considerably important (Ekanayake *et al.* 2015).

In our study, nests associated with cameras were less predated than nest without them, for similar vegetation conditions. This may suggest an influence of the use of cameras in nest predation. Meek *et al.* (2016) also found that camera traps were intrusive for predators and predator responses varied from repulsion to attractiveness in relation to the cameras. However, some predators displayed no awareness of cameras, further supporting the dependence on predator composition. Another study

found no evidence of camera placement having an effect on predation levels, although this was conducted mainly in forest landscapes (Stirnemann *et al.* 2015).

Our results also revealed a moderately diverse predator composition, with at least 17 different species of predators being identified in predation events, a value that we could safely assume to be higher, since we were unable to reliably identify some species. Corvids (particularly the Carrion crow) played a major role in nest predation, being present in slightly over half of the identified predation events. It is known that these birds can associate cameras and other nest markers used by scientists to locate real nests through observation and use this advantage for egg predation (Rollinson & Brooks 2007; Ekanayake *et al.* 2015), which could justify the relative importance of both of these factors in predicting nest predation rates in our study (**Table 8**).

Although this study was successful in identifying a good number of predators, the number of events was not nearly enough to obtain significant information on individual predator species' behaviour patterns. For instance, other studies revealed the Egyptian mongoose as a potentially important nest predator in farmland landscapes with consequences on a range of bird species (Lewis *et al.* 2011; Beja *et al.* 2014) and its effect was correlated with that of Red fox (Beja *et al.* 2014). Since we recorded only 2 predation events for each of these species, we could neither support nor deny such conclusions, though these species could have contributed to the differences in predation rates across grasslands and forests. The exception was the Carrion crow which confirmed its status as a ubiquitous predator since it predated nests in every day of the experiment at all habitat types and highly influenced how predation rates varied across a range of increasing vegetation height around the nest, especially in grassland habitats.

There is still a severe lack of knowledge of many aspects of nest predator foraging habits, predator communities and the interactions between nest predators and habitats (Ibáñez-Álamo *et al.* 2015). Predator identification should be a critical starting point to all studies investigating nest predation interactions of a species or community (Ibáñez-Álamo *et al.* 2015). The increasing availability of cheaper technology will certainly allow more researchers to monitor nests 24 hours a day using a similar system to ours, which will provide access to the identity and foraging behaviour of nest predators, as well as quantitative data on their prevalence and role in nest losses (Cox *et al.* 2012). Thus, we believe more studies should implement similar measures, since knowing predator identity not only provides a better understanding of the selective pressures influencing parental and offspring antipredator strategies, but also clarifies how habitat

management affects both individual predators and predator communities (Lyons *et al.* 2015).

4.3. The success of corvids as predators

Tree plantations resulting from afforestation act as sources of generalist predators of various types, including rodents, lagomorphs and corvids (Batary & Baldi 2004; Pita *et al.* 2009; Reino *et al.* 2010a; Sánchez-Oliver *et al.* 2014). From our results, it is clear that corvids were dominant predators, being determinant in shaping predation rates in our study area. A recent study in another region of southern Portugal also found corvids having great impacts on predation rates, although it concluded that ground nests were mainly predated by mammals (Beja *et al.* 2014). These generalists are powerful nest predators and thrive in mosaic habitat landscapes such as our study area, where they exhibit an exploratory behaviour (Pita *et al.* 2009; Reino *et al.* 2010a; Ekanayake *et al.* 2015). Tendencies of agricultural intensification, have also been suggested to benefit corvids while being deleterious for a wide range of other species (Barnett *et al.* 2004). Furthermore, urban areas surrounding farmlands have been increasing and also represent a source of ubiquitous and opportunistic nest predators such as corvids and others (Sánchez-Oliver *et al.* 2013), since they have the ability to supplement their diets with non-seasonal anthropogenic food sources when eggs are not available (Ekanayake *et al.* 2015). Interestingly, corvid species were shown to have larger brains than urban-avoider species (Carrascal *et al.* 2014) which seems to indicate that these animals are behaviourally innovative species that have higher success and experience lower mortality than others, when exposed to a novel environment (Sol *et al.* 2008). Indeed, there is evidence indicating they possess the ability to learn not only through observation, but also from the behaviour of other corvids (Ekanayake *et al.* 2015). All previously mentioned factors might therefore help us understand their importance when predicting predation rates (**Table 8**, **Figure 11**) in a context where they were clearly abundant predators (see **Table 7**). Furthermore, the severity of their predatory impacts on a range of bird species is, therefore, likely to continue increasing.

Other studies elsewhere have showed increases in prey numbers when corvid control was performed (Peery & Henry 2010) and controlling both corvid and fox populations seemed to have dramatically increased reproductive success of ground-nesting birds in a particular study (Fletcher *et al.* 2010).

To better understand the severity of predatory impact, not only of corvids but also

other impactful predators, further investigation is warranted. Perhaps focusing more on an extensive cover of predators, relating camera traps with predator abundance samplings. Even the relevance of a single nest predator can vary among habitats (Ekanayake *et al.* 2015). Thus, a critical first step in mechanistic studies of nest predation in human altered landscapes is the identification of each major nest predator which, while logistically challenging, is sure to pay large dividends in understanding nest predation risk (Cox *et al.* 2012; Ekanayake *et al.* 2015).

4.4. Implications on conservation of open farmland birds

The poor implementation and monitoring of the CAP throughout the years is a major concern since few were the funds directed towards agri-environment schemes (less than 5%), many of those do not have the restoration of farmland wildlife populations as a key objective and their effects are generally poorly monitored (Donald *et al.* 2006). However, where they were properly designed, targeted and monitored, with the assessment of biodiversity impacts being made a priority, these schemes usually revealed benefits to biodiversity (Peach *et al.* 2001; Vickery *et al.* 2001). Initiatives such as the LIFE Nature Programme, which pose a major cost to society, show only mixed effects on long-term conservation of farmland birds (Santana *et al.* 2014). Some flagship species, being the main targets of these initiatives, are benefited by this program. However, such is not the case for several other species (some of conservation concern) such as farmland, ground-nesting and steppe bird species, which possess contrasting habitat requirements (Santana *et al.* 2014) and would probably benefit from a partial reversion of fields within the agricultural landscape to semi-natural grassland, an initiative that has been difficult to justify to landowners on an economic basis, despite its conservation benefits on flora and fauna (Gooch *et al.* 2015).

For the particular case of the Mediterranean open farmlands, afforestation should be largely avoided (Reino *et al.* 2010a), mainly in areas of higher conservation priority. Instead, promoting a mosaic of arable crops and pastures may be key in conserving conditions for farmland species. To reduce the impacts on edge-avoiding steppe birds while still maintaining the development of rich bird assemblages, authors suggest a spatial configuration of forest patches that minimize edge effects by afforesting a small number of relatively large patches instead of the usual practice of planting several small forest patches across the landscape (Reino *et al.* 2009). A more generalized use of pine pruning, which speeds up the development of the tree layer, should also benefit overall species density during winter (Sánchez-Oliver *et al.* 2013), since an under-

developed tree layer benefits several species characteristic of open farmland habitats (such as Calandra lark and Little bustard) and some forest species that are of interest to hunters (Jedlicka *et al.* 2011). Additionally, mosaic management can be implemented by attempting to coordinate management across a group of farmlands rather than concentrating on individual farms, which has been shown as beneficial for ground-nesting birds (Gooch *et al.* 2015). Moreover, although predator control is often aimed at reducing predation on game species, it may also benefit ground-nesting birds, as controlled carnivore species frequently predate on nests and chicks of these avian species (Fletcher *et al.* 2010).

Finally, nest predator communities may confound our ability to achieve a comprehensive assessment of the effects of habitat manipulations on nest predation patterns, as we have previously discussed (Lyons *et al.* 2015), and therefore complicate management actions aimed at reducing nest loss rates (Ellison *et al.* 2013).

Climate change will also potentially impose additional complexity in terms of clarifying the causes of nest predation since it is likely to interact synergistically with other environmental stressors to shape distribution and behaviour of co-occurring predators and prey (Ibáñez-Álamo *et al.* 2015). Thus, characterization of the role of predator identity in the relationship between bird nest failure and habitat characteristics is more relevant than it has ever been and will likely be very important in future conservation efforts.

5. Conclusion and Future perspectives

Local and landscape patterns were concurrent with what is known of the SPA of Castro Verde, namely: afforestation resulting in habitat fragmentation, agricultural intensification of farmlands and consequential effects of mowing and livestock grazing.

Farmland areas nearby pine woodlands had higher predation risks, comparing to the other tree stands, which implies a detrimental effect of the increasingly widespread afforestation with the former. Although contradictory to similar studies, its negative effect on ground-nesting birds is generally supported since afforestations with pinewoods have a higher impact on biodiversity due to a contrast with natural Mediterranean woodlands, which possess lower tree cover and higher structural heterogeneity. Though one might expect similar impacts from *Eucalyptu*s stands, they are often very old stands, smaller in area and sometimes not evenly distributed across the whole area. Landscape type, *i.e.,* identity of surrounded forest stands, appeared to be more important in shaping nest predation rates than edge effects, which is expected since there is increasing support for landscape context over edge effects, in recent times. However, the main defining features shaping nest predation patterns were nest site manipulation, vegetation height and the occurrence of Carrion crow. Indeed, predation probability highly decreased with vegetation height whereas nest-site manipulation severely increased predation probability resulting in a much less pronounced predation probability vs. vegetation height decline curve. This is mostly corroborated by some studies (*e.g.* Beja *et al.* 2014; Huhta *et al.* 2015), supporting that local variables strongly influence the number of predated nests as well as other predation related parameters (*i.e.,* days until predation).

We found, contrary to several claims, that the use of cameras (or other type of nest-site manipulation) to detect predators may influence predation rates, whereas the use of artificial nests *per se* seemed mostly non-influential. Artificial nests are generally criticized when used to extrapolate predation rates or predator abundances for real nests. Our study supports that, when used simultaneously with camera traps, this method is one of few ways to effectively identify a wide range of predators as well as spatial and temporal differences in nest predation patterns, if used correctly. We hypothesized that major differences found in relation to several other studies were mainly due to predator community composition. Despite being able to identify a moderately diverse number of predators, we believe that many others could have remained unidentified. Furthermore, predator identification did not reveal a great deal of information on predatory behaviours. However, even with a relatively small number

of predation events, corvids still revealed some patterns, mostly supporting their well-known ubiquity. Their abundant numbers relative to other predators might also reflect their superior intelligence compared to other predators, as well as their capability of taking advantage of the current state of development of the Mediterranean farmland, which may justify their influence on altering nest predation rates when present.

We conclude that nest predation rates in the Mediterranean farmlands of Castro Verde can be predicted to an extent, by a limited set of local variables. However, to improve knowledge of nest predation patterns, characterization of predator identity in each landscape is an expensive but determining factor that should be taken into account in future targeted management efforts. Furthermore, there is a serious bias in terms of studies which focus on temperate regions, while tropical regions are underrepresented (Vetter *et al.* 2013), a problem that should be exacerbated by climate change.

Indeed, the study of nest predation now constitutes a vital part of research in different areas, including Population Ecology, Ethology, Evolution and Conservation. The constant debate and improvement of field techniques together with the advancements in technology should help managers to identify a suite of actions that are more appropriate to the local and landscape conditions.

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Annexes

Annex i. Factor loadings on the six axes with eigenvalues > 1.0 extracted by a PCA of landscape variables after a varimax normalized rotation, and the proportion of variance that each axis accounts for. Each variable is represented as a measure for each Study Patch. Abbreviations are as follows: Annual crops and pastures (ACP); Open woodland (OW); Permanent crops (PC) and Woodland (W). Values in Bold indicate factor loadings > |0.70|.

Variables	PC1	PC2	PC3	PC4	PC5	PC6
Core area of ACP	0.46	-0.02	**-0.86**	-0.12	0.04	-0.01
Number of ACP patches	0.01	0.06	-0.20	**0.93**	0.13	0.06
Average Patch Size of ACP	0.22	-0.07	-0.25	**-0.88**	-0.09	-0.01
Edge Density of ACP	0.35	0.15	-0.48	0.42	0.57	0.06
AWMSI of ACP	0.08	0.11	0.30	-0.50	0.65	0.01
Core area of OW	0.18	-0.08	**0.96**	0.01	-0.11	0.04
Number of OW patches	0.08	0.10	0.42	0.01	**0.81**	0.09
Average Patch Size of OW	0.19	-0.01	0.32	-0.15	**-0.78**	0.10
Edge Density of OW	0.09	0.01	**0.91**	0.07	0.28	0.19
AWMSI of OW	-0.16	0.04	0.19	-0.01	-0.02	**0.85**
Core area of PC	-0.09	**0.90**	0.07	-0.04	-0.01	-0.19
Number of PC patches	0.12	**0.78**	-0.10	0.03	0.23	0.24
Average Patch Size of PC	-0.01	**0.80**	0.08	0.07	-0.19	-0.18
Edge Density of PC	0.03	**0.95**	-0.03	-0.03	0.15	0.07
AWMSI of PC	0.11	**0.77**	-0.15	0.01	0.10	0.42
Core Area of W	**-0.97**	0.01	-0.02	0.07	0.05	-0.01
Number of W patches	**-0.89**	-0.01	0.02	0.17	-0.03	0.24
Average Patch Size of W	**-0.73**	-0.12	-0.07	0.11	-0.03	-0.20
Edge Density of W	**-0.95**	0.02	0.09	0.08	-0.03	0.17
AWMSI of W	-0.19	-0.06	0.14	0.49	-0.10	-0.07
% explained variance	18.74	18.16	16.54	11.98	11.35	6.15